

Anatomical Review and Preliminary Phylogeny of the Facelinid Nudibranchs (Opisthobranchia: Aeolidina) of the Taxon *Phyllodesmium* Ehrenberg, 1831

DELISSE M. ORTIZ

School of Earth and Environmental Science, Washington State University Vancouver, 14204 NE Salmon Creek Avenue, Vancouver, WA 98686-9600, USA
(e-mail: ortiz@vancouver.wsu.edu)

TERRENCE M. GOSLINER

Department of Invertebrate Zoology and Geology, California Academy of Sciences, 875 Howard Street, San Francisco, CA 94103, USA
(e-mail: tgosliner@calacademy.org)

Abstract. The anatomy and morphology of species of *Phyllodesmium* are described for *P. parangatum* Ortiz and Gosliner, 2003, *P. magnum* Rudman, 1991, *P. poindimiei* (Risbec, 1928), *P. hyalinum* (Ehrenberg, 1831), *P. crypticum* Rudman, 1981, *P. serratum* (Baba, 1949), *P. colemani* Rudman, 1991, *P. kabiranum* Baba, 1991, *P. macphersonae* Burn, 1962, *P. briareum* (Bergh, 1896), *P. longicirrum* (Bergh, 1905), *P. pecten* Rudman, 1981, *P. opalescens* Rudman, 1991, *P. horridum* (Macnae, 1954), *P. iriomotense* Baba, 1991 and *P. guameusis* Avila *et al.* A phylogenetic analysis supports the monophyly of *Phyllodesmium*. Species possessing an unbranched digestive tract are most basal, while more derived taxa have a highly ramified digestive tract. More basal species form a grade with symplesiomorphies such as an unbranched digestive tract, jaw with many denticles, absence of zooxanthellae and elongate foot corners. The remaining species have elaborate digestive tracts and have undergone morphological and physiological changes allowing the storage of zooxanthellae in the cerata, for use as a secondary food source. It is evident from this study that morphological changes occurring within *Phyllodesmium* correlate closely with their increased association with symbiotic zooxanthellae. This first parsimony-based phylogenetic study of *Phyllodesmium* largely supports the scenario of morphological evolution first proposed by Rudman (1991).

INTRODUCTION

Within the Aeolidina, the most diverse taxon is the Facelinidae with more than 130 described species. One highly specialized group, species of *Phyllodesmium* Ehrenberg, 1831, has received considerable attention owing to the trophic specialization and evolution of symbiosis of members of this taxon. The facelinid taxon *Phyllodesmium* includes nineteen described species, almost all of which are known to be specialized predators on alcyonarian octocorals restricted to the Indo-Pacific tropics and adjacent temperate regions (Rudman, 1981b; Rudman, 1991; Gosliner *et al.*, 1996; Avila *et al.*, 1998; Ortiz, 2001; Ortiz & Gosliner, 2003; Burghardt & Wägele, 2004; Burghardt & Gosliner, 2006). The fact that most of these species also contain symbiotic zooxanthellae and exhibit a range of variation in the elaboration of digestive gland structures to accommodate this symbiosis, makes them ideal candidates for phylogenetic and comparative biological studies. It needs to be determined if *Phyllodesmium*

represents a monophyletic group and, if this proves to be the case, this particular study can illuminate the nature of the evolution of symbiosis within this particular clade.

Species currently placed in *Phyllodesmium* have been placed in several different genera including *Phestilla* Bergh, 1874, *Cratena* Bergh, 1864, *Hervia* Bergh in Mörch, 1871, *Aeolidia* Cuvier, 1798, *Myrrhine* Bergh, 1905, *Favorinus* Gray, 1850, *Godiva* Macnae, 1954, *Ennoia* Bergh, 1896, *Phyllodesmiopsis* Risso-Dominguez, 1964, and *Babiella* Risso-Dominguez, 1964, reflecting the confusion surrounding the systematics of this group. Rudman (1981, 1991) summarized much of this confusion and the historical review will not be repeated here.

Since the late 1800s, there has been a substantial amount of biological interest and research regarding ecological interactions and symbiosis between the dinoflagellate zooxanthellae *Symbiodinium* Freudenthal, zooxanthellae, and a number of different marine hosts. This literature deals mostly with scler-

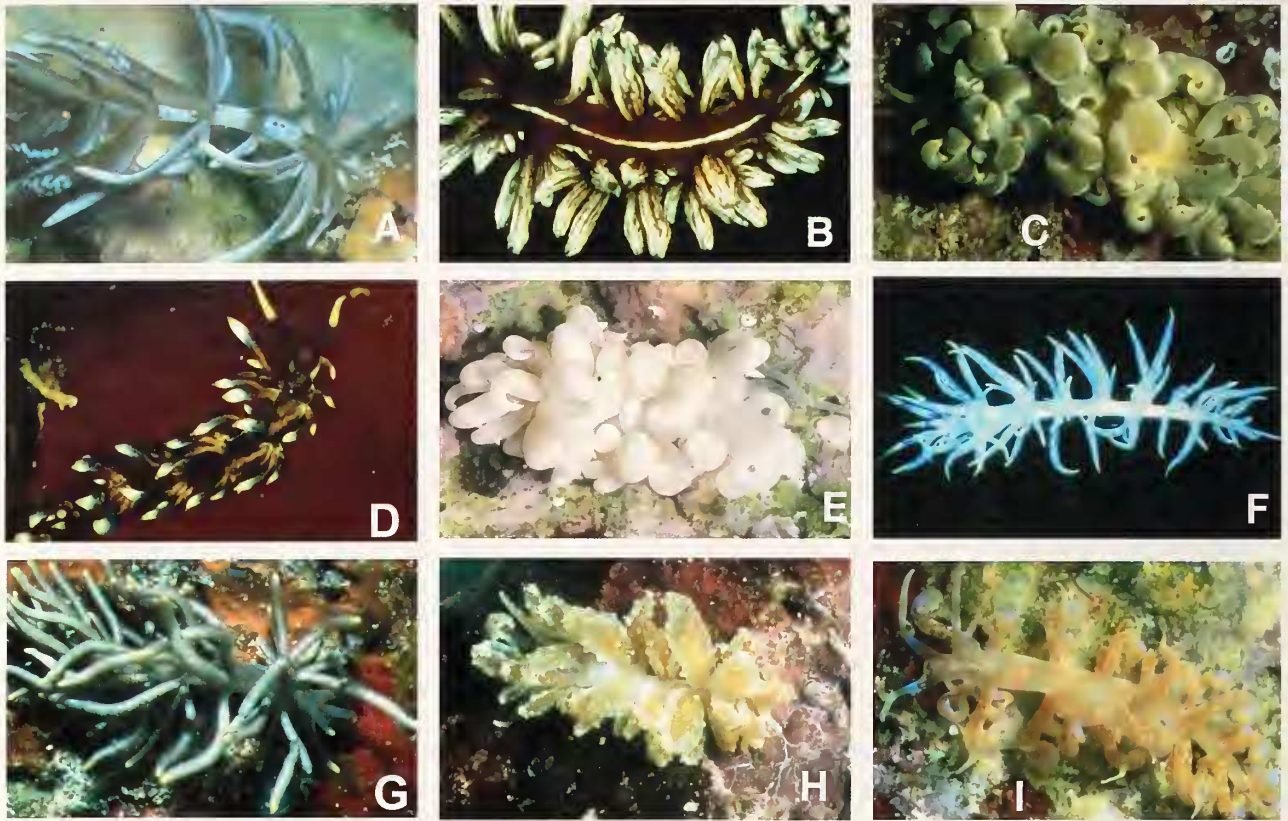


Figure 1. Living animals of *Phyllodesmium* species. A. *P. colemani*, photo by T.M. Gosliner. B. *P. kabiraman*, photo by R.F. Bolland. C. *P. magnum*, photo by T.M. Gosliner. D. *P. macphersonae*, photo by R.F. Bolland. E. *P. parangatun*, photo by T.M. Gosliner. F. *P. serratum*, photo by R.F. Bolland. G. *P. briareum*, photo by T.M. Gosliner. H. *P. crypticum*, photo by T.M. Gosliner. I. *P. poindimiei*, photo by T.M. Gosliner.

actinean corals and species of venerid clams in the taxon *Tridacna* Bruguière (Fankboner, 1971; Goreau *et al.*, 1973; Fitt and Trench, 1981; and many others), but has since expanded into the realm of nudibranch and coelenterate symbiosis. Two examples are Rudman (1982), who worked on the aeolidoidean and arminoidean nudibranch mollusks and Kempf (1984) who studied species of *Melibe* Rang, *Pteraeolidia* Bergh and *Berghia* Trinchese. Hoegh-Guldbergh & Hinde (1986) also examined nudibranch-zooxanthellae symbiosis; they studied the effects of the presence of zooxanthellae on their nudibranch host. Recent works by Burghardt & Wägele (2004, 2006), Burghardt *et al.* (2005), and Burghardt & Gosliner (2006) have examined photosynthetic activity in a variety of additional opisthobranchs, including several species of *Phyllodesmium*.

The available literature, however, has dealt mostly with associations regarding nudibranch and dinoflagellate symbiosis in a descriptive form. Research on the evolution of aeolid nudibranchs and their specific hosts is virtually absent from the literature. Aside

from the work of Rudman (1981a, 1981b, 1982, 1987, 1991), publications regarding evolutionary adaptations as a result of morphological modifications to accommodate the respective symbionts are rare. No phylogenetic study based on the ecological interaction between a facelinid nudibranch taxon and its host has been published. The preliminary phylogeny of the facelinid nudibranchs belonging to the taxon *Phyllodesmium* Ehrenberg, 1831 is the first such study.

The various adaptations and other anatomical variations, which have evolved in species of *Phyllodesmium*, have resulted in it becoming one of the most morphologically diverse in the Aeolidina (Figure 1; Rudman, 1991). The reconstruction of phylogenies within the aeolid nudibranchs has been problematic. Difficulties have been encountered by those systematists that have attempted to clarify the phylogeny of aeolids (Miller, 1974; Gosliner and Ghiselin, 1984). Historically, the branching of the digestive gland, reflected in the ceratal arrangement, and the position of the anus, has been greatly emphasized in the

classification of the Aeolidina (Odhner, 1934). Miller (1971) also considered the "branching of the digestive gland and position of the anus to be main features for delineating genera." The taxon *Phyllodesmium*, as well as its nominal species, have been delineated and described based on these characters. However, Rudman (1991) related ceratal arrangement, digestive gland branching, and other major interspecific morphological characters to the ecology of their food sources.

The purpose of this study is to fully review and supplement the anatomy of species of *Phyllodesmium* in order to produce a preliminary phylogenetic analysis. The results of this study can be used as a basis for examining morphological changes within *Phyllodesmium* in response to coevolution with zooxanthellae symbiosis.

MATERIAL AND METHODS

Morphological Studies

Specimens of previously described species of *Phyllodesmium*, accompanied by color slides of the living animals, were the primary source for morphological characters used in this study. Most importantly, examination of the material housed at the California Academy of Sciences (CASIZ) and the Australian Museum (AM) provided a wealth of specimens that were used to assess and verify doubtful and uncertain characters, as well as developing new characters for the phylogenetic analysis.

Species of Facelinidae were examined and compared morphologically, using reproductive and radular morphology, and anatomical features including ceratal arrangement and structure, location of anus, branching of ceratal digestive gland, and shape of the anterolateral foot corners. Individual specimens were dissected to examine detailed structure of the cerata, buccal mass, and reproductive system. Dissections and scale drawings were made using a dissecting microscope with a camera lucida. An incision was made along the entire midline of the foot. The reproductive systems, as well as external features (e.g., rhinophores, anterior and posterior foot, location of anus, ceratal arrangement, etc.) were then examined.

A LEO series 1400 Scanning Electron Microscope (SEM) at the California Academy of Sciences (CAS) was used to make scaled digital pictures of the structure of the radulae and jaws, in order to survey the phylogenetic characters used in the study. The cerata were dissected and stained. An average of 3 to 4 cerata were extracted from the dorsum of some of the specimens representing several species. Micrographs of the ceratal digestive branching were digitally captured using a Kodak MDS 100 camera

mounted on an M400 Wild microscope. Some of the more problematic cerata were drawn to scale (using a camera lucida on a Nikon SMC-10 dissecting microscope) or photographed (using an FX-35 DX Nikon camera mounted on an SMZ-U Nikon dissecting microscope). The cerata of one species, *Phyllodesmium crypticum*, were stained with a solution of acid fuchsin and 70% ethanol, dehydrated in alcohol, cleared with xylene, and mounted in Permount on a microscope slide.

Phylogenetic Analysis

Taxa. For the phylogenetic analysis, 20 taxa have been considered (Table 1). In order to determine polarity of morphological change within *Phyllodesmium*, specimens of *Godiva quadricolor* (Barnard, 1927) and *Favorinus japonicus* Baba, 1949, were selected as outgroup taxa based on the fact that they represent relatively underived members of the Facelinidae (Willan, 1987). In the absence of a more comprehensive phylogeny of the Facelinidae, we agree with Willan (1987) that these taxa represent appropriate outgroups for polarizing characters within *Phyllodesmium*. These data were compared with the descriptions of *G. quadricolor* from Willan (1987) and *F. japonicus* from Rudman (1980).

Phylogenetic Methods

To develop a phylogenetic hypothesis for *Phyllodesmium*, the morphological data were entered into a data matrix using MacClade 3.01 (Maddison and Maddison, 1992). All the characters used were assigned equal weight and treated as unordered. PAUP 4.0b4a (Swofford, 2000) was used for phylogenetic reconstruction using a heuristic search with the TBR branch swapping option. One hundred random start trees were obtained by stepwise addition. Three characters were deleted in the subsequent analyses due to being uninformative and ambiguous (14, 21 and 30). The deleted characters are indicated in parenthesis in the character description section. Bremer decay analyses were performed by subsequent analysis with a series of iterations that examined successive trees, each one step longer, to estimate branch support using the methodology of Bremer (1994).

Characters. The 31 characters used to resolve the phylogeny of *Phyllodesmium* are listed in Table 2. Of these characters, twenty-nine are binary and two are multistate. The characters states are represented with numbers: 0, "presumed" plesiomorphic condition; 1–2, "presumed" apomorphic conditions (refer to Table 3).

Table 1

Sources used to describe the species in the present study. Abbreviations: R80, (Rudman, 1980); R81b, (Rudman, 1981b); R91, (Rudman, 1991); B37, (Baba, 1937); B91a,b, (Baba, 1991a,b); Bu62, (Burn, 1962); M54, (Macnae, 1954); Rb28, (Risbec, 1928); Be05, (Bergh, 1905); C98, (C. Avila et al., 1998); RC87, (R.C. Willan, 1987); E31 (Ehrenberg, 1831); Br04 (Burghardt et al., 2004); Br06 (Burghardt 2006); T.G., Terrence Gosliner; R.F.B., Robert F. Bolland; PNG, Papua New Guinea; l.r., literature review; p.p., published pictures; p.s., present study; N/A, Non Applicable.

<i>Phyllodesmium</i> species	CASIZ Accecion #	Slide #	Reference	Type of research
<i>P. poindimiei</i>	086009, 93947	T.G.: 086009	Rb28, R91, p.s.	Re-examined
<i>P. parangatu</i>	T.G.: 106472,105657, 96325, 103702, 105676	T.G.: 105676, 106472,96325,105657	p.s.	New Species
<i>P. magnum</i>	79239,79221	PNG-1988	R91, p.s.	Re-examined
<i>P. hyalinum</i>	69970, 68731	R.F.B 2161	E31, Be05, B37, R81b, R91, M54, p.s.	Re-examined
<i>P. horridum</i>	N/A	p.p.	R81b, R91, M54	l.r.
<i>P. crypticum</i>	99314, 106465	Station 35 Ligpo	R81b, R91, p.s.	Re-examined
<i>P. serratum</i>	114759	<i>P. serratum</i> /Okinawa	B91a, R91, p.s.	Re-examined
<i>P. colemani</i>	110358	T.G.: 110358	R91, p.s.	Re-examined
<i>P. kabiraum</i>	89035, 103793	R.F.B. 3158	B91b, p.s.	Re-examined
<i>P. macphersonae</i>	115724, 104700, 65346	R.F.B. 3304	R91, R81b, Bu62, p.s.	Re-examined
<i>P. longicirrum</i>	N/A	p.p.	R81b, R91	l.r.
<i>P. pecten</i>	N/A	p.p.	R81b	l.r.
<i>P. opalescens</i>	N/A	p.p.	R91	l.r.
<i>P. iriometense</i>	N/A	p.p.	B91b	l.r.
<i>P. guamensis</i>	N/A	p.p.	C98	l.r.
<i>P. briareum</i>	65346, 65299, 83678	PNG-1988	R91, p.s.	Re-examined
<i>P. jakobsenae</i>	N/A	p.p.	Br04	l.r.
<i>P. rudmani</i>	N/A	p.p.	Br06	l.r.
<i>G. quadricolor</i>	N/A	p.p.	RC87, B27	l.r.
<i>F. japonicus</i>	N/A	p.p.	R80, B49	l.r.

SYSTEMATIC DESCRIPTIONS

Introductory Remarks

Species descriptions include anatomical information derived from the present study and from literature review. The anatomical data derived from other references have been repeated for a comparison with the data obtained from this study. The data for the re-examined specimens is from original research for the present study, unless otherwise stated in the text. Some morphological characters, such as the distribution and storage of zooxanthellae, could not be determined by the dissections performed, hence literature review was necessary.

Family Facelinidae Bergh, 1889

Phyllodesmium Ehrenberg, 1831

Phyllodesmium Ehrenberg, 1831 [type species by subsequent designation (Gray, 1847), *Phyllodesmium hyalinum* Ehrenberg, 1831]

Myrrhine Bergh, 1905 [type species by monotypy, *Myrrhine longicirra* Bergh, 1905]

Babiella Risso-Dominguez, 1964 [type species by monotypy, *Herzia serrata* Baba, 1964]

Phyllodesmiopsis Risso Dominguez, 1964 [type species by monotypy, *Favorinus horridus* Macnae, 1954]

Diagnosis: Alcyonarian-eating aeolids with cerata capable of being autotomized. Cerata slightly or extremely flattened, lacking functional cnidosacs (a synapomorphy for *Phyllodesmium*). Oral glands absent with a pair of discrete tubular salivary glands present. Rhinophores smooth or slightly nodular (a synapomorphy for *Phyllodesmium*). Foot corners angular (a synapomorphy for *Phyllodesmium*). Ceratal arrangement variable. Pre-cardiac cerata arranged in single or double rows, while the post-cardiac cerata arranged in single or double rowed arches, simple rows, or a mixture of simple row arches and simple rows. Cleioproctic anus present in first post-cardiac arch or behind first postcardiac arch. Masticatory border or jaw with a single row of denticles or smooth (a synapomorphy for *Phyllodesmium*). Radular formula 0.1.0. Teeth usually having long pointed central cusp or reduced one. Each cusp with lateral flange along each side, with or without denticles. Genital opening below anterior limb of first right pre-cardiac arch or row. Reproductive system with single receptaculum seminis.

Table 2
Character descriptions and character states of present study.

1. Body size 0 = moderate 1 = large	12. Anterior foot corners 0 = elongate 1 = angular	23. Radular denticle location 0 = along masticatory border of tooth 1 = extent to central cusp of tooth
2. Branching of digestive gland 0 = absence of branched duct 1 = slightly branched duct 2 = highly branched duct	13. Vertical position of anus on first postcardiac group 0 = posterior 1 = dorsally	24. Base of teeth 0 = long 1 = short
3. Storage of zooxanthellae 0 = absent 1 = present	14. Rhinophore size 0 = long 1 = extended	25. Radular base of teeth 0 = long 1 = short
4. Ceratal surface 0 = smooth 1 = nodular	15. Rhinophore surface 0 = swelling on lamaelle 1 = smooth or slightly nodular	26. Denticle size on jaw plates 0 = small 1 = large
5. Ceratal shape 0 = cylindrical 1 = flattened 2 = smooth	16. Masticatory border of jaw 0 = several rows of denticles 1 = single row of denticles	27. Cnidosome 0 = present 1 = absent
6. Ceratal apex 0 = blunt 1 = curled	17. Number of denticles 0 = numerous 1 = few and elongate	28. Penial spine 0 = present 1 = absent
7. Ceratal arch in precardiac group 0 = present 1 = absent	18. Cusp of teeth 0 = short 1 = long	29. Female gland mass 0 = elongate 1 = bulbous
8. First postcardiac arrangement 0 = arches 1 = rows	19. Radular denticles 0 = present 1 = absent	30. Penial complex 0 = large 1 = small
9. Second postcardiac arrangement 0 = arches 1 = single or double rows	20. Radular denticle arrangement 0 = separated 1 = tightly congested	31. Arrangement of radular denticles 0 = single rows 1 = double rows
10. Third postcardiac arrangement 0 = arches 1 = single or double rows	21. Radular denticle length 0 = long 1 = short	
11. Foot width 0 = wide 1 = narrow	22. Radular denticle tip 0 = blunt 1 = pointed	

Prostate forming gland mass at the base of penis. Penis simple, unarmed.

Phyllodesmium parangatum Ortiz & Gosliner,
2003

(Fig. 1E)

Material examined: Holotype, California Academy of Sciences, CASIZ 106472 near Twin Rocks, Anilao, Batangas Province, Luzon, Philippines, 15 April 1996, T. Gosliner. Paratypes: three specs, one dissected, CASIZ 105657, Devil's Point, Maricaban Island, Batangas Province, Luzon, Philippines, 25.3 m depth, 23 February 1995, T. Gosliner. One specimen dissected, CASIZ 105676, Bonito Island, Maricaban Island, Batangas Province, Luzon, Philippines, 2.1 m depth, 27 February 1995, T. Gosliner. One specimen, CASIZ 96325, Cemetary Beach, Maricaban Island, Batangas

Province, Luzon, Philippines, 13 March 1994, T. Gosliner.

Distribution: So far, known only from the original localities in the Philippines.

Remarks: The anatomy of this species is completely described by Ortiz and Gosliner (2003).

Phyllodesmium magnum Rudman, 1991

(Figs. 1C, 2A–C)

Phyllodesmium sp. Orr, 1981: 69.

?*Phyllodesmium* sp. Willan and Coleman, 1984: 48, fig. 154.

Phyllodesmium magnum Rudman, 1991: 190–193, figs. 20A, B, 22–24, 27C, D, 28, 29.

Material examined: Two specimens, one dissected, CASIZ 79239, Horseshoe Cliffs, 1 km WNW of Onna

Table 3

Character states present in *Phyllodesmium* species. Data code: see Table 2. Abbreviation: ?, no data available.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>P. horridum</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1
<i>P. serratum</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
<i>P. poindimiei</i>	0	1	0	0	0	1	0	1	1	1	1	1	0	0	1	2	1	1
<i>P. opalescens</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0
<i>P. briareum</i>	0	2	1	0	0	0	1	1	1	1	1	1	0	1	1	2	?	1
<i>P. colemani</i>	0	2	1	0	1	0	0	1	1	1	1	1	0	1	1	2	?	1
<i>P. magnum</i>	1	2	1	0	1	1	1	1	1	1	0	1	0	1	1	2	?	1
<i>P. hyalinum</i>	0	2	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1
<i>P. crypticum</i>	0	2	1	1	1	1	0	0	0	0	0	1	0	0	1	1	1	1
<i>P. macphersonae</i>	0	2	1	0	0	1	0	1	1	1	1	1	0	1	1	2	?	1
<i>P. longicirrum</i>	1	2	1	0	1	1	0	1	1	1	0	1	0	1	1	2	?	1
<i>P. pecten</i>	0	2	1	1	1	1	0	0	1	1	0	1	0	0	1	1	1	1
<i>P. iriomotense</i>	0	1	1	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0
<i>P. kabiranum</i>	1	2	1	0	1	1	0	0	0	0	0	1	0	0	1	1	1	1
<i>P. parangatm</i>	1	2	?	0	1	1	1	1	1	1	0	1	0	0	1	1	1	1
<i>P. guamensis</i>	1	2	1	0	1	1	1	1	1	1	0	1	0	1	1	2	?	1
<i>G. quadricolor</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>F. japonicus</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. jakobseni</i>	1	2	1	0	1	1	?	?	?	?	0	1	0	0	1	1	1	1
<i>P. rudmani</i>	1	2	1	0	0	0	1	1	1	1	0	1	0	0	1	1	1	1

	19	20	21	22	23	24	25	26	27	28	29	30	31
<i>P. horridum</i>	0	1	0	1	0	1	0	0	1	0	?	1	0
<i>P. serratum</i>	0	1	0	1	0	1	1	0	1	0	?	?	0
<i>P. poindimiei</i>	1	1	0	0	0	1	1	1	0	?	1	1	1
<i>P. opalescens</i>	0	0	0	0	0	0	0	0	1	0	1	0	0
<i>P. briareum</i>	0	0	1	1	1	1	0	?	1	0	0	0	0
<i>P. colemani</i>	0	0	1	1	1	1	0	?	1	0	1	0	0
<i>P. magnum</i>	1	1	1	0	1	1	1	?	1	0	1	1	0
<i>P. hyalinum</i>	0	0	1	1	1	0	0	1	1	0	1	0	0
<i>P. crypticum</i>	0	0	1	1	1	1	0	1	1	0	1	1	0
<i>P. macphersonae</i>	0	0	1	0	1	0	0	?	1	0	0	1	0
<i>P. longicirrum</i>	1	1	1	1	1	1	1	?	1	0	1	0	0
<i>P. pecten</i>	0	1	0	1	0	1	1	1	1	0	1	1	0
<i>P. iriomotense</i>	0	0	0	0	0	1	1	1	1	0	?	?	0
<i>P. kabiranum</i>	0	0	1	0	1	1	1	1	1	0	1	0	0
<i>P. parangatm</i>	0	1	0	0	0	1	1	1	1	0	0	0	0
<i>P. guamensis</i>	0	1	1	1	1	1	?	?	1	0	1	1	1
<i>G. quadricolor</i>	0	0	0	0	0	0	0	0	0	1	1	0	0
<i>F. japonicus</i>	0	0	0	0	0	1	0	0	0	0	?	?	0
<i>P. jakobseni</i>	0	1	1	1	1	1	1	1	1	0	0	0	0
<i>P. rudmani</i>	0	1	1	1	1	1	1	1	1	0	0	0	0

Village, Okinawa, Ryukyu Islands, Japan, 1.5 m depth, 6 May 1991, R.F. Bolland. One specimen, dissected, CASIZ 79221, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 6 May 1991, R.F. Bolland.

Distribution: Type locality is New Caledonia, however its distribution is widespread. Northern Western Australia, Marshall Islands and Hong Kong (Rudman, 1991). Collected from Tanzania, Papua New Guinea, Philippines and Japan (Gosliner *et al.*, 1996; present study).

External morphology (Fig. 1C): Body large, broad, up to 120 mm (Rudman, 1991). Present specimens (CASIZ 79239 and CASIZ 79221) 45 mm and 68 mm in length, respectively; elongate body extending broadly from the anterior end, tapering at posterior end. Foot corners, long, angular. Oral tentacles, rhinophores slender, smooth. Cerata large, smooth, flattened and curved apically, extending all along the animal's dorsum. Ceratal arrangement consisting of single vertical rows on distinctive ridges, double row of precardiac cerata along each side of body. Reproductive opening below right-sided double precardiac rows.

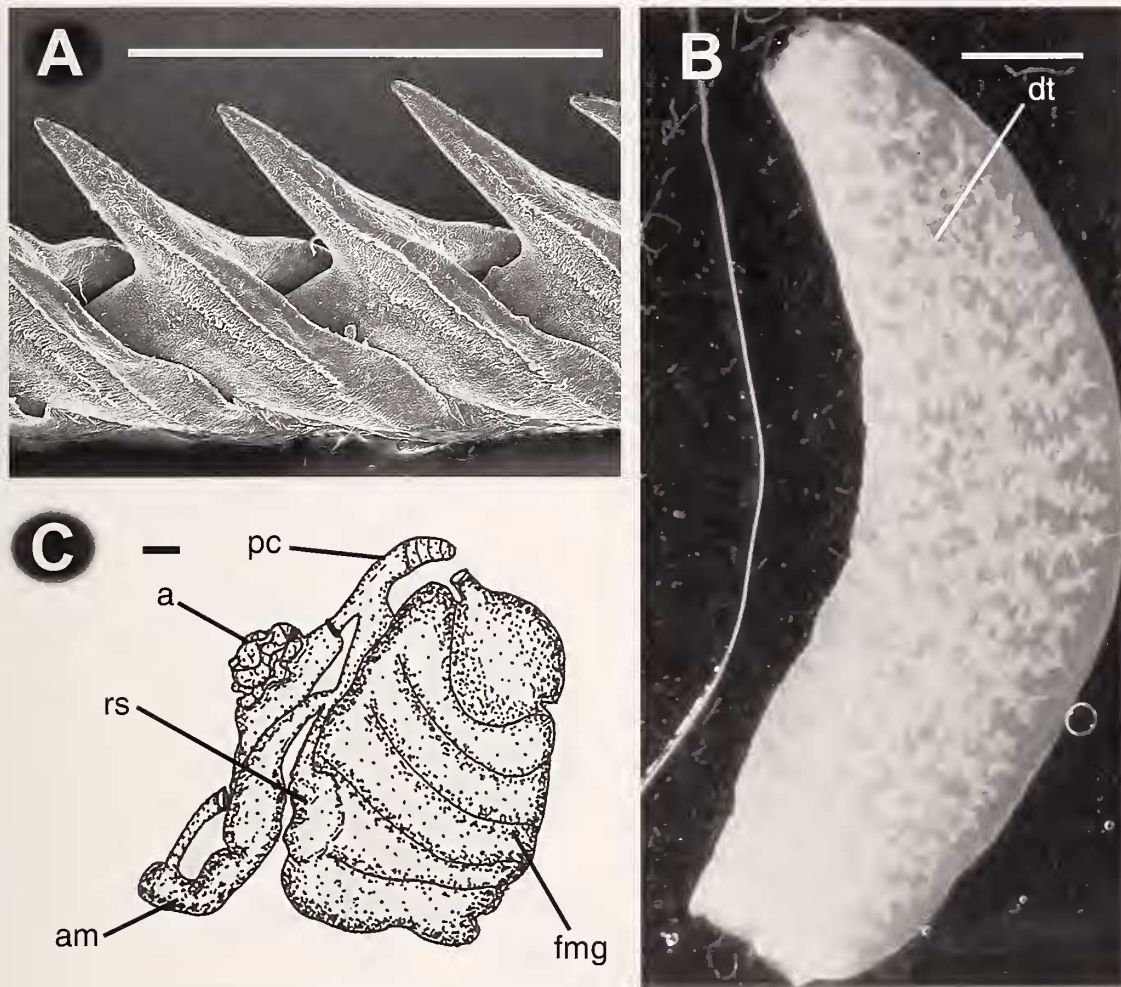


Figure 2. *Phyllodesmium magnum*. **A**. Lateral view of radula. **B**. View of digestive tract in a cerata. **C**. Reproductive System. Abbreviations: a, albumen gland; am, ampulla; rs, receptaculum seminis; pc, penial complex; fmg, female mass gland; dt, digestive tract. Scale bars: **A** = 0.50 mm; **B** = 10 mm; **C** = 5 mm.

Renal opening on right side and centred within interhepatic space. Anal papilla between right postcardiac cerata and behind uppermost cerata of first postcardiac row on prominent mound. Up to 11 postcardiac rows present with up to 8 or more cerata per row.

Cerata and digestive gland (Fig. 2B): Cerata flattened, providing increase of surface area, allowing for the branching of the digestive gland duct on each cerata. Digestive gland extending all along cerata with numerous branches diverging into many secondary and tertiary branches. Flattened branches with terminal chambers; zooxanthellae present in parts of cerata exposed to sunlight, including digestive gland in both the body wall and foot (Rudman, 1991).

Buccal armature (Fig. 2A): Radular formula of 45 mm long specimen $21 \times 0.1.0$ (CASIZ 79239). Tooth short,

with wide base enclosing part of basal posterior structure. Cusp elongate, pointed. Denticles small, short, continuous, extending halfway down each tooth. Jaw with smooth masticatory border (Rudman, 1991).

Reproductive system (Fig. 2C): Preampullary duct long, narrow, extending into a broad, long folded ampulla via thin duct. Duct bifurcating into receptaculum seminis and penial complex. Penial complex extending into short, narrow prostate, connecting to membrane gland via small opening. Prostate with overlying layer of tissue, connecting with a massive, folded and bulbous female gland mass.

***Phyllodesmium poindimiei* (Risbec, 1928)**

(Figs. 11, 3A–C)

?*Phidiana tenuis* Eliot, 1905: 287–288.

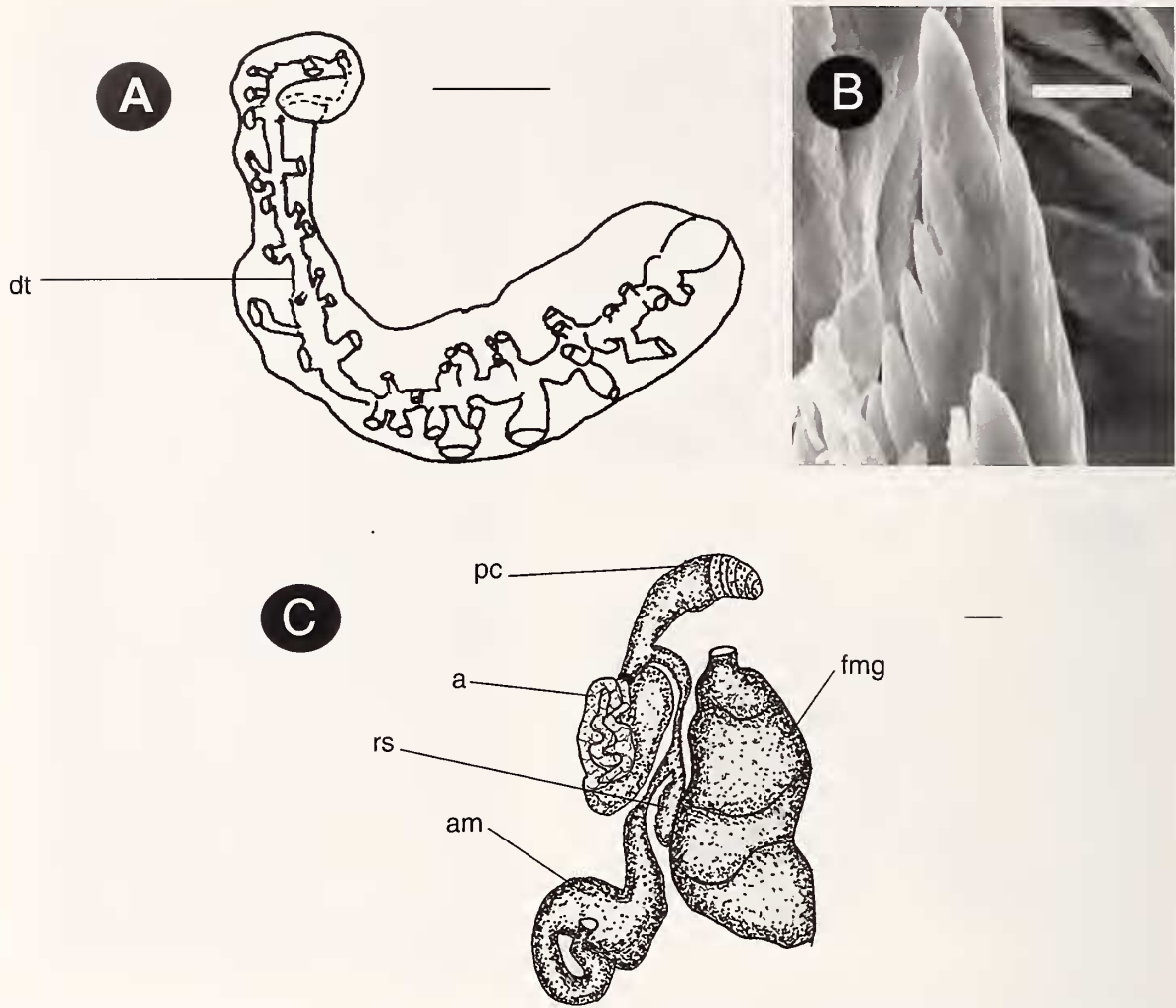


Figure 3. *Phyllodesmium poindimiei*. A. View of digestive tract inside a ceras. B. Radular denticles. C. Reproductive system. Abbreviations: a, albumen gland; am, ampulla; rs, receptaculum seminis; pc, penial complex; fmg, female mass gland; dt, digestive tract. Scale bars: A = 10 mm; B = 0.002 mm; C = 5 mm.

Aeolidia poindimiei Risbec, 1928: 246–247, fig. 78, Pl. 9, fig. 3.

Phestilla poindimiei — Risbec, 1953: 138–139, figs. 93–96.

Phyllodesmium poindimiei — Rudman, 1981b: 224–229, figs. 3–7, 21B, 25C, 27.

Material examined: Three specimens, CASIZ 86009, Devil's Point, NW side of Maricaban Island, Batangas, Luzon Island, Philippines, 25.3 m depth, 26 March 1993, T.M. Gosliner. One specimen, CASIZ 105746, Sepok, Maricaban Island, Batangas Province, Luzon, Philippines, 16.7 m depth, 24 February 1995, T.M. Gosliner. One specimen, dissected, CASIZ 93947, Kurlup Island, Watubela Islands, E Banda Sea,

Moluccas, Indonesia, 12.1 m depth, 11 November 1993, P. Fiene.

Distribution: Originally described from New Caledonia (Risbec, 1928). Found and redescribed from New South Wales and Western Australia (Rudman, 1991). Specimens also collected from Indonesia, Japan, and the Philippines (present study).

External morphology (Fig. 11): Body of moderate size, elongate, 13.5 mm in length. Body shape wider anteriorly, extending narrowly from anterior to posterior end. Anterior foot narrow anteriorly. Foot corners angular. Rhinophores moderately long, smooth, approximately equal in length size to oral tentacles. Cerata cylindrical, smooth and curved, similar to *P.*

magnum and *P. parangatum*. Dorsum partially exposed, not covered by numerous recurved cerata. Ceratal arrangement, except for the precardiac arch, of single rows with up to 3 to 5 recurved cerata each, on right side of body. Both renal and reproductive openings immediately below precardiac arch, in close proximity to first postcardiac row within interhepatic space. Anal papilla immediately below first postcardiac row. Postcardiac rows ranging from 7 to 9 rows on each side of dorsum.

Cerata and digestive gland (Fig. 3A): Ceratal digestive gland duct extending to apical end of each ceras, branching outwardly in close proximity to ceratal wall. Simple branching ducts perpendicular to central duct, extending in terminal sac in variable manner. Cerata cylindrical, smooth, terminating in curled apex.

Buccal armature (Fig. 3B): Radular formula $24 \times 0.1.0$ (CASIZ 93947). Tooth broad with long base, extending anteriorly and encasing posterior edge of adjacent tooth. Cusp long, with denticulation, extending along centre edge of margin. Degree of separation between elongate, adjacent denticles variable. Masticatory border of jaw smooth (Rudman, 1991).

Reproductive system (Fig. 3C): Preampullary duct long, broad, extending into bulbous ampulla via thin duct. Duct bifurcating into receptaculum seminis and into penial complex. Penial complex extending into large, short, bulbous prostate. Connection between albumen and membrane glands basal. Prostate connecting with folded. Female gland mass long, massive.

Remarks: Rudman (1981) considered the likelihood that *Phidiana tenuis* (Eliot, 1905) may be a senior synonym of *Phyllodesmium poindimiei* based on similarities of external morphology and radula. He was reluctant to place these taxa in formal synonymy, pending the collection of additional material from East Africa, the type locality of *P. tenuis*. We concur with this approach to resolving the nomenclature of this species.

Phyllodesmium hyalinum Ehrenberg, 1831

(Fig. 4A–D)

Phyllodesmium hyalinum Ehrenberg, 1831: 32.

Phyllodesmium xeniae Gohar & Aboul-Ela, 1957: 131–144, P1.1

Favorinus horridus brevitentaculatus Engel and van Eeken, 1962: 28–29, fig. 5.

Phyllodesmium orientale Baba, 1991b:109, figs. 1–3 ; pl. 1, fig. 1, possible synonym.

Material examined: One specimen, CASIZ 69970, Seragaki Beach, 1.3 km ENE of Maeki-zaki, Okinawa, Ryukyu Islands, Japan, 1.5 m depth, 13 May 1989,

R.F. Bolland. Two specimens, one dissected, CASIZ 68731, Hole in the Wall, near Hussein Village, north of Madang, north coast, Papua New Guinea, 6.4 m depth, 21 July 1989, T.M. Gosliner.

Distribution: First described from the Red Sea (Ehrenberg, 1831), but has been recorded more recently from the Philippines (Bergh, 1905), Japan (Baba, 1937), Tanzania (Rudman, 1981b), South Africa (Gosliner, 1987), Papua New Guinea, Japan, Tanzania, Indonesia (present study).

External morphology: Body of moderate size, 10.3 mm in length. Foot wide, extending posteriorly, tapering into reduced posterior end. Oral tentacles long, about equal to the length of smooth rhinophores. Curved cerata numerous, covering surface of dorsum. Ceratal arrangement in arches in precardiac and postcardiac cerata. Number of cerata per arch 7 to 10 on each side of dorsum. Reproductive opening situated at base of precardiac arch, on right side of dorsum. Renal opening centred in the interhepatic space, in close proximity to first postcardiac arch. Anal papilla on a distinctive mound located on right side of the dorsum, outside arch on the posterior side of the first postcardiac arch. Up to six postcardiac ceratal arches present on each side of the body.

Cerata and digestive gland (Fig. 4C): Digestive gland extending entire length of ceras with secondary and tertiary branches extending in “web-like form” parallel to ceratal wall. Ceratal surface nodular. Branches terminating in small chambers, assumed to be the storage areas for the zooxanthellae from its alcyonacean feeding source, *Xenia* spp. (Rudman, 1991). Nodular cerata flattened and curled apically.

Buccal armature (Figs. 4A–B): Radular formula $25 \times 0.1.0$ (CASIZ 68731). Tooth narrow with long base, elongate cusp. Denticles visible halfway down tooth. Denticles short, pointed, well separated. Jaws with single row of large, sparse denticles all along masticatory border (Rudman, 1991).

Reproductive system (Fig. 4D): Preampullary duct short, expanding into elongate, bulbous ampulla via narrow duct. Duct bifurcating into receptaculum seminis and penial complex. Penial complex extending into large, elongate, folded prostate. Prostate connecting to folded albumen gland, with surrounding membrane gland, and massive and long female gland mass.

Remarks: *Phyllodesmium orientale* Baba, 1991 was described as a distinct species (Baba, 1991b) based on two specimens collected from Japan. Baba noted that it was similar to *P. hyalinum*, except that it has an anal position that is more similar to *P. crypticum*. However,

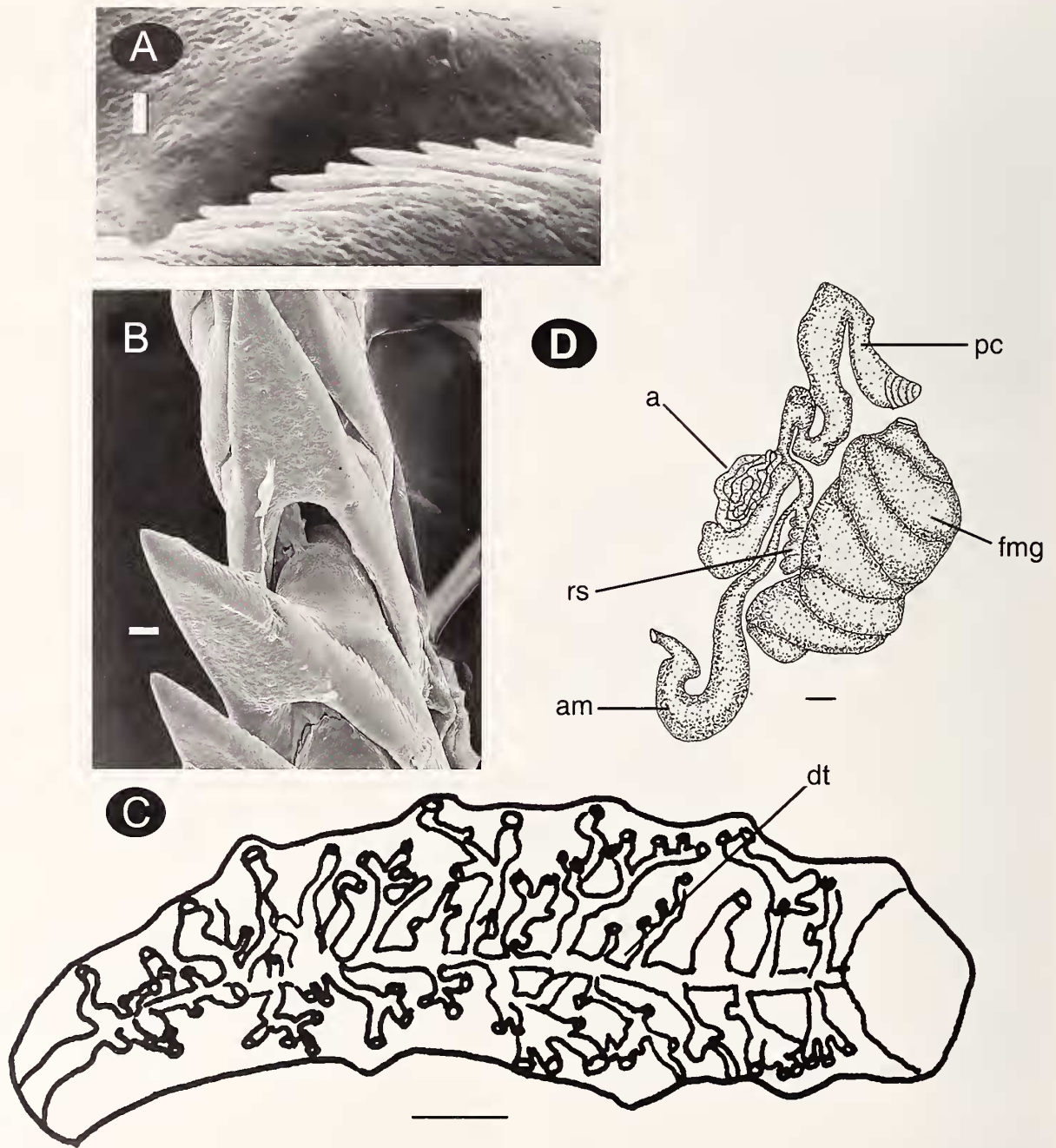


Figure 4. *Phylloidesmium hyalinum*. **A.** Denticles on masticatory border of radula. **B.** Anterior view of radular tooth. **C.** View of digestive tract inside a ceras. **D.** Reproductive system. Abbreviations: a, albumen gland; am, ampulla; rs, receptaculum seminis; pc, penial complex; fmg, female mass gland; dt, digestive tract. Scale bars: **A** = 0.010 mm; **B** = 0.003 mm; **C** = 5 mm; **D** = 5 mm.

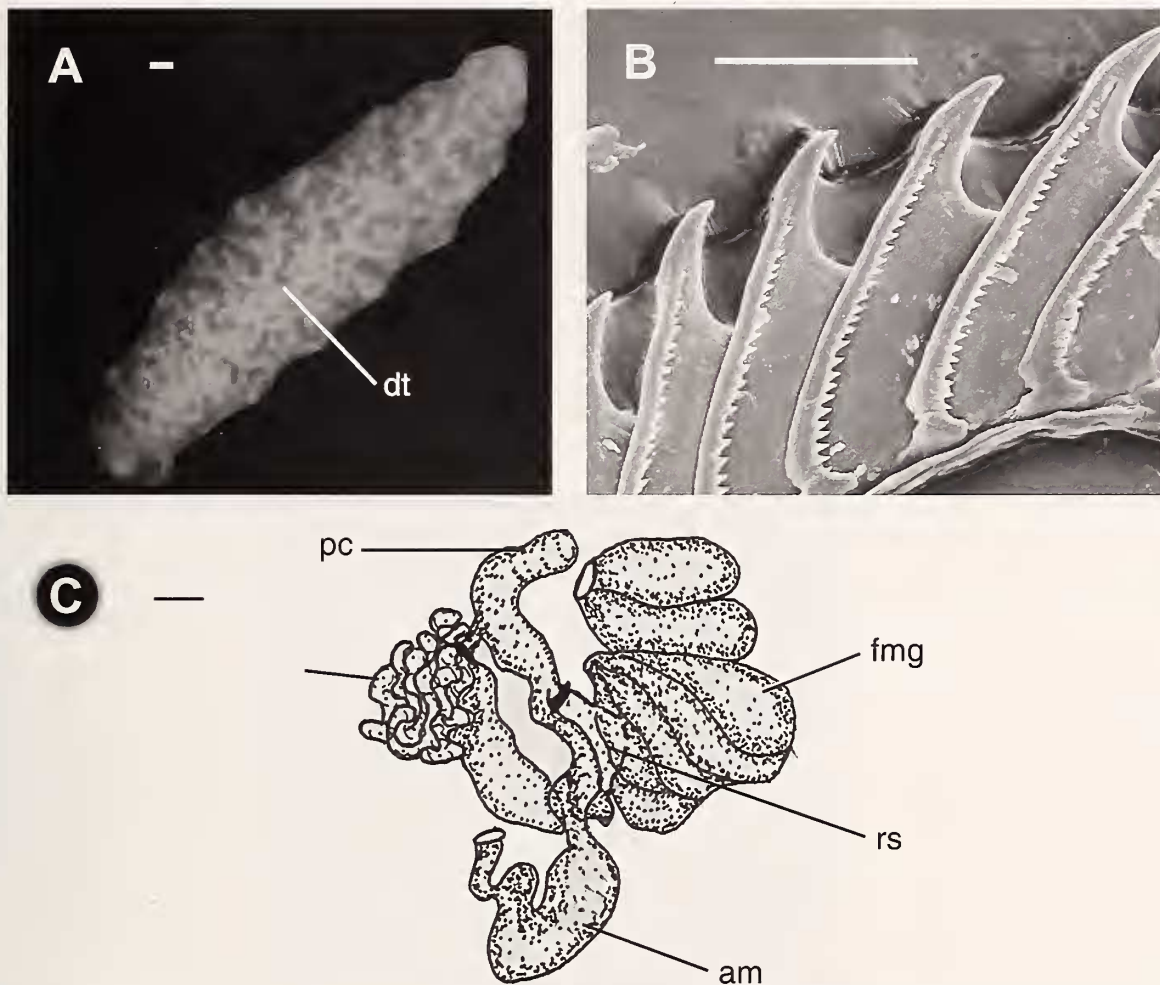


Figure 5. *Phylloidesmium crypticum*. **A.** View of digestive tract inside a ceras. **B.** Lateral view of radula. **C.** Reproductive system. Abbreviations: a, albumen gland; am, ampulla; rs, receptaculum seminis; pc, penial complex; fmg, female mass gland; dt, digestive tract. Scale bars: **A** = 10 mm; **B** = 0.05 mm; **C** = 5 mm.

it is evident from Baba's illustration (pl. 1, fig. 1) that the anus is rather dorsal in its position, similar to *P. hyalinum*. We suspect that *P. orientale* is synonymous with *P. hyalinum* and list it as a probable synonym, pending discovery of more material from Japan.

***Phylloidesmium crypticum* Rudman, 1981**

(Figs. 1H, 5A–C)

Phylloidesmium cryptica Rudman, 1981b: 232–236, 244–261, figs. 10A, B, 11, 12D, 13, 14B, 22B, 23, 26B, 27; Rudman, 1991: 194, fig. 28.

Material examined: One specimen, dissected, CASIZ 99314, Huamja Island, NE side Manua, Mtwara Region, Tanzania, 4 November 1994, T.M. Gosliner. Two specimens, one dissected, CASIZ 106465, near

Twin Rocks, Batangas Province, Luzon, Philippines, 9.1 m depth, 15 April 1996, T.M. Gosliner.

Distribution: Originally described from Dar es Salaam, Tanzania (Rudman, 1981b). Recorded from New South Wales and Western Australia (Rudman, 1991). Specimens collected from Philippines and Japan (present study).

External morphology (Fig. 1H): Body of moderate size, 10 mm in length. Foot wide, elongate, tapered at posterior end. Anterior foot corners tapered. Rhinophores, oral tentacles smooth and long; rhinophores shorter than oral tentacles. Cerata numerous often obscuring dorsum of body. Ceratal arrangement in arches. Number of cerata undetermined due to detachment of most of the cerata of the material examined. Up to 7 postcardiac arches present on each

side of the body. Reproductive opening situated below anteriormost portion of right precardiac arch. Renal opening immediately in front of uppermost portion of the right-sided first postcardiac arch. Anal papilla located within first postcardiac arch, on right side of body.

Cerata and digestive gland (Fig. 5A): Digestive gland extending all along ceras. Ceratal surface nodular with secondary and tertiary branches extending in a "web-like form" to the ceratal wall. Branches terminating in small chambers, assumed to be the storage area for the zooxanthellae extracted from its alcyonacean prey, *Xenia* spp. (Rudman, 1991). Cerata flattened, curved at apex.

Buccal armature (Fig. 5B): Radular formula $24 \times 0.1.0$ (CASIZ 106465). Tooth with broad, elongate base, extending anteriorly to adjacent tooth. Cusp elongate extending anteriorly. Short, pointed, well-separated denticles present on all teeth. Single row of large denticles present on masticatory border of jaw plates.

Reproductive system (Fig. 5C): Preampullary duct short, extending into long, folded, bulbous ampulla. Ampulla extending via broad duct to receptaculum seminis and penial complex. Penial complex small, with proximal end connecting to massive and folded albumen and membrane glands. Distal end connecting with small, irregular and bulbous female gland mass.

Remarks: *Phyllodesmium hyalinum* and *P. crypticum*, may easily be confused as the same species, but differ in the base of the teeth, anal position, rhinophore size and size of penial complex. *Phyllodesmium hyalinum* has greatly extended rhinophores, an anus located above the first postcardiac arch, a narrow base and a large penial complex. *Phyllodesmium crypticum* has moderately long rhinophores. The anus is inside the first postcardiac arch. The radular teeth have a wide base and the penial complex is small.

***Phyllodesmium serratum* (Baba, 1949)**

(Figs. 1F, 6A–C)

Hervia serrata Baba, 1949: 105–106, 179, pl. 46, figs. 156–157, text figs. 142–143.

Cratena serrata — Baba, 1955: 36, 56.

Babiella serrata — Risso-Dominguez, 1964: 223.

Phyllodesmium serrata — Rudman, 1981b: 260.

Phyllodesmium serratum — Baba, 1991a: 101, figs. A–H; pl. 1 figs. 1–3).

Material examined: One specimen dissected, CASIZ 114759, 1 km WNW of Onna Village, Horseshoe Cliffs, Okinawa, Ryukyu Islands, Japan, 44.2 m depth, 18 May 1994. R.F. Bolland.

Distribution: Originally described from Japan (Baba, 1949). Recorded from different regions of Australia: Victoria, New South Wales and parts of the Northern Territory (Rudman, 1991).

External morphology (Fig. 1F): Body, 32 mm in length, moderate size. Foot wide and elongate, tapering posteriorly, tapered anterior foot corners. Rhinophores smooth and moderately long, as long as the oral tentacles. Cerata, smooth, long, straight, extending across whole body, arranged in arches, precardiac arch can have up to five cerata on each side, postcardiac arches range from 7 to 10 arches on each side, each arch containing up to 7 cerata on each arch. Reproductive opening between center and uppermost edge below precardiac arch. Renal opening in front of first postcardiac arch. Anal papilla on a distinctive mound, centred inside first postcardiac arch.

Cerata and digestive gland (Fig. 6A): Branched digestive gland, extending as finger-like projection inside cerata, short lateral branches evident, cerata are cylindrical, smooth, long and numerous.

Buccal armature (Figs. 6B–C): Radular formula $24 \times 0.1.0$ (CASIZ 114759). Tooth wide with short base, extending anteriorly and covering the posterior basal edge of the tooth in front, long cusp, denticulation extending all along border of each tooth. Tightly joined and long denticles, extending into pointed tip, small denticles on masticatory border of jaw plates (Baba, 1991a).

***Phyllodesmium colemani* Rudman, 1991**

(Figs. 1A, 7A–B)

Phyllodesmium sp. Coleman, 1988: 14–15, 1989: 7, 54.
Phyllodesmium colemani Rudman, 1991: 187–190, figs. 14C, 18, 19, 20C–E, 21, 27–29.

Material examined: Two specimens, one dissected, CASIZ 110358, Bus Stop Reef, Balayan Bay, Batangas Province, Luzon Island, Philippines, 23 April 1997, M. Miller.

Distribution: Known from its type locality, Lord Howe Island, Coral Sea (Rudman, 1991) and the Philippines (present study).

External morphology (Fig. 1A): Body 22.5 mm in length, of moderate size, extending uniformly narrowly from anterior to posterior end. Foot narrow and elongate. Rhinophores greatly extended and smooth, similar to oral tentacles. Cerata long, smooth, flattened, extending along dorsum of body, visible dorsum. Ceratal arrangement with single postcardiac vertical rows and precardiac arch, up to 3 to 4 cerata on each of the 7 to 8 postcardiac rows located on each side of body, up to 3 to 5 cerata on each side on precardiac

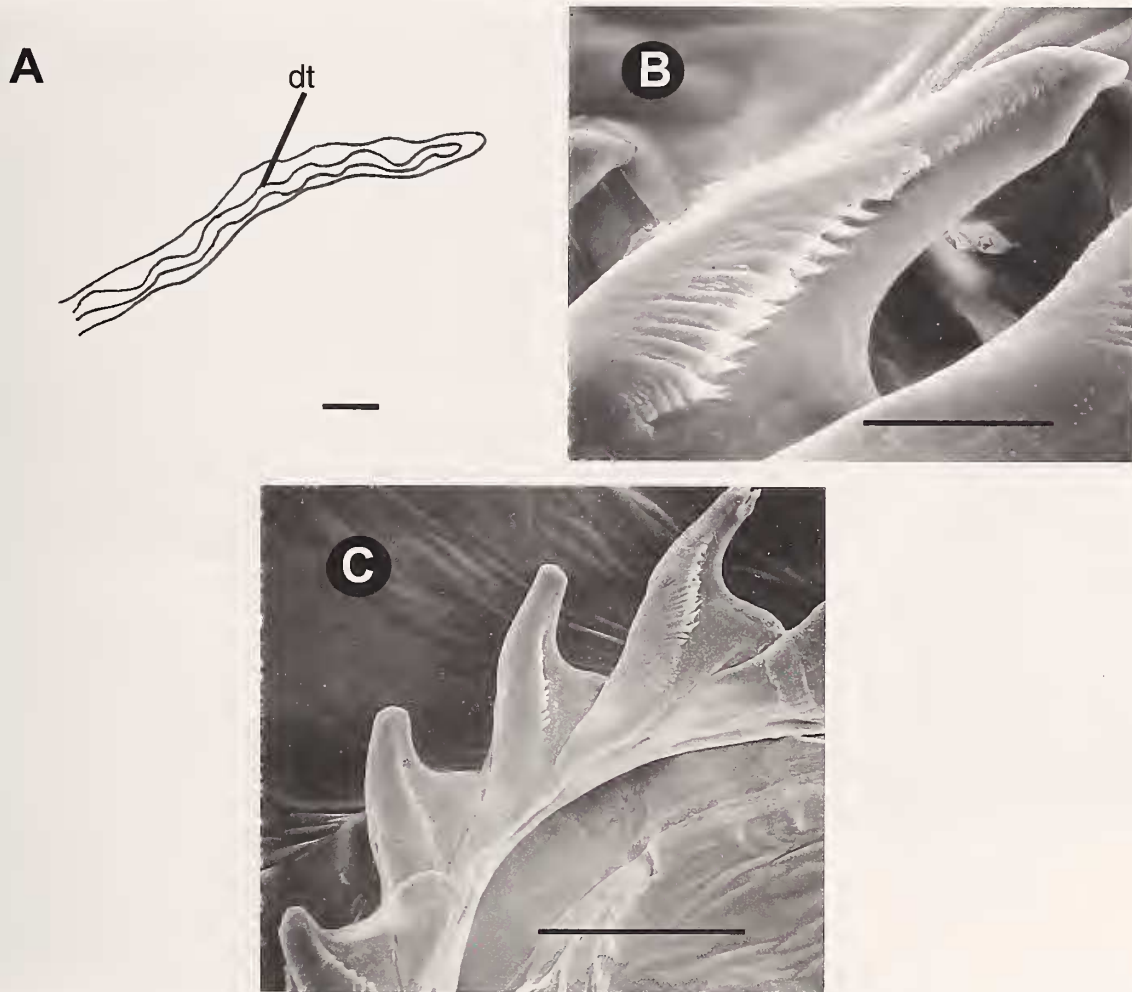


Figure 6. *Phyllodesmium serratum*. A. View of digestive tract inside a cerata. B. Lateral view of radula and its denticles. C. Lateral profile of radula. Abbreviations: dt, digestive tract. Scale bars: A = 5 mm; B = 0.02 mm; C = 0.07 mm.

arch. Reproductive opening, renal opening, and anal papilla located on right side of body. Reproductive opening located below anterior-most portion of pre-cardiac arch, renal opening located in center of interhepatic space; anal papilla raised on a distinctive mound, located outside first postcardiac row.

Cerata and digestive gland (Fig. 7A): Cerata long, slender, flattened, smooth. Ceratal apex blunt. Digestive gland extending all along cerata through central duct; central duct bifurcating into perpendicular secondary branches terminating in bilateral and broad branches. Upon examination of translucent ceratal tissue, the uniformity and extent of the branching is visible.

Buccal armature (Fig. 7B): Radular formula $26 \times 0.1.0$ (CASIZ 110358). Tooth wide and long, base extending anteriorly, covering posterior portion of front tooth. Cusp long and narrow in anterior portion of the tooth. Denticles visible on central part of each tooth, short

and separate from each other, terminates in pointed tip; smooth masticatory border of jaw (Rudman, 1991).

Reproductive system: Reproductive system similar to that described for the other species of *Phyllodesmium*, although, as in *P. opalescens*, the prostate gland is very large (Rudman, 1991).

Phyllodesmium kabiramm Baba, 1991

(Figs. 1B, 8A–D)

?*Eolida bella* Rüppell & Leuckart, 1831: 35, Pl. 1. 10, fig. 4.

?*Phyllodesmium bellum* — O'Donoghue, 1929: 715.

Phyllodesmium kabiramm Baba, 1991b: 113, figs. 4–5, Pl. 1, fig. 2.

Material examined: One specimen, CASIZ 89035, Seragaki Beach, 1.3 km ENE of Maeki-zaki, Okinawa.

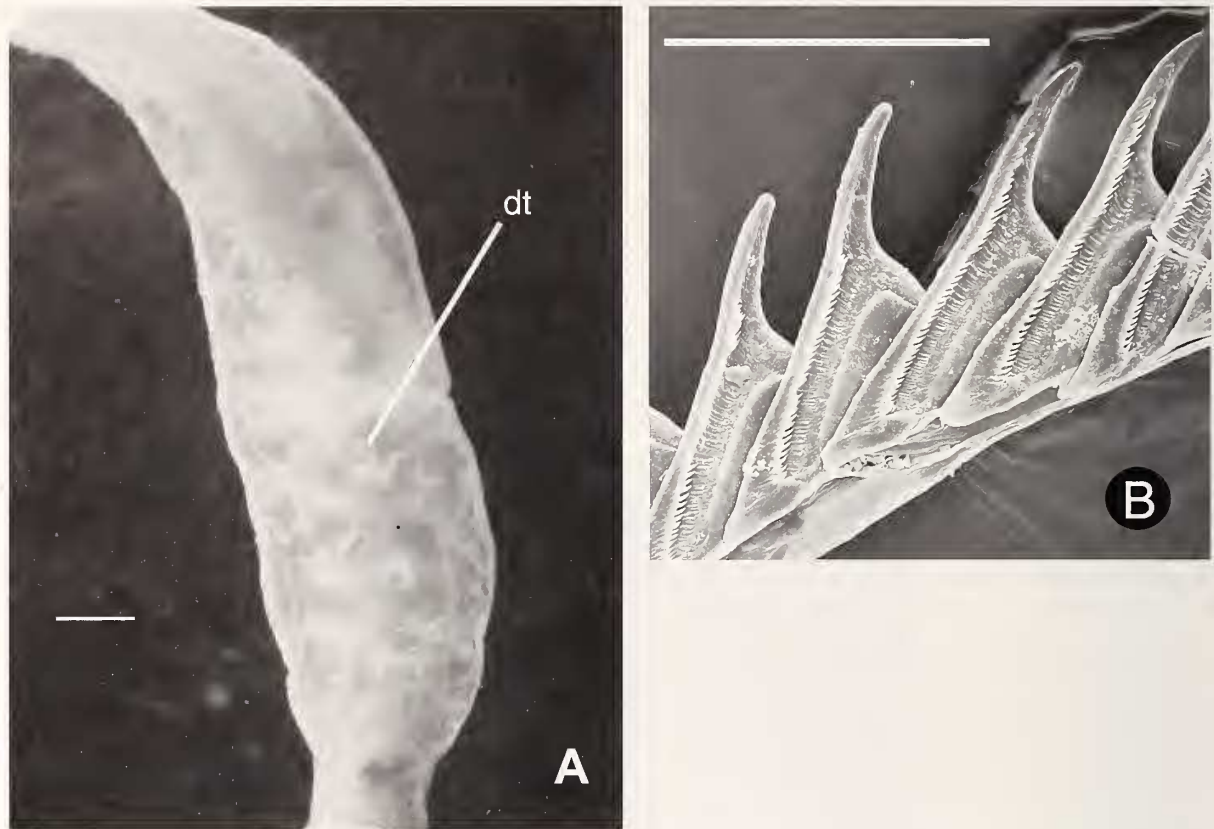


Figure 7. *Phylloidesmium colemani*. A. View of digestive tract inside a cerata. B. Lateral view of radula. Abbreviations: dt, digestive tract. Scale bars: A = 5 mm; B = 0.02 mm.

Ryukyu Islands, Japan, 1.5 m depth, 3 April 1993, R.F. Bolland. Two specimens, one dissected, CASIZ 103793, Cathedral Rock, Balayan Bay, Batangas Province, Luzon Island, Philippines, no depth, 25 February 1995, D.W. Behrens.

Distribution: Known from its type locality Okinawa, Japan (Baba, 1991b) and the Philippines (present study).

External morphology (Fig. 1B): Body 56 mm in length, large in size, narrowing uniformly from anterior to posterior end, wide foot, smooth and moderately long rhinophores, oral tentacles shorter in size than rhinophores. Cerata flattened, smooth, with a straight apex, extending outwardly covering the whole dorsum. Ceratal arrangement of one precardiac arch and single vertical rows on each side of the body, lying on distinctive ridges, up to 7 to 8 cerata on each precardiac arch on each side of the body, 8 to 11 cerata on each of the 7 to 9 postcardiac single arches on each side dorsum. Reproductive opening found in right side of dorsum, right below and inside precardiac arch. Renal opening is in interhepatic space, right above the most basal posterior edge of the first postcardiac arch. Anal

papilla on distinctive mound, between first and second postcardiac arches on right side of body.

Cerata and digestive gland branching (Fig. 8C): Cerata flattened, smooth, terminating in a curled apex. Digestive gland branching into secondary and tertiary branches; numerous multiple branches that extend in "web-like" manner, terminating in close proximity to the body wall. Ducts terminate in small chambers, capable of harboring zooxanthellae. Dark brownish-green color present likely due to presence of zooxanthellae in the cerata (Baba, 1991b).

Buccal armature (Figs. 8A–B): Radular formula $63 \times 0.1.0$ (CASIZ 89035). Base of tooth short and wide, long cusp. Denticles visible along center of tooth, separated, short, with blunt tip; masticatory border of the jaw plates has large denticles.

Reproductive system (Fig. 8D): Preampulla duct narrow, long; expanding into large, bulbous, folded ampulla. Ampulla divides into receptaculum seminis and penial complex by thin duct. Penial complex large, connecting to massive and folded albumen gland, opening to a folded, long prostate. Prostate connecting

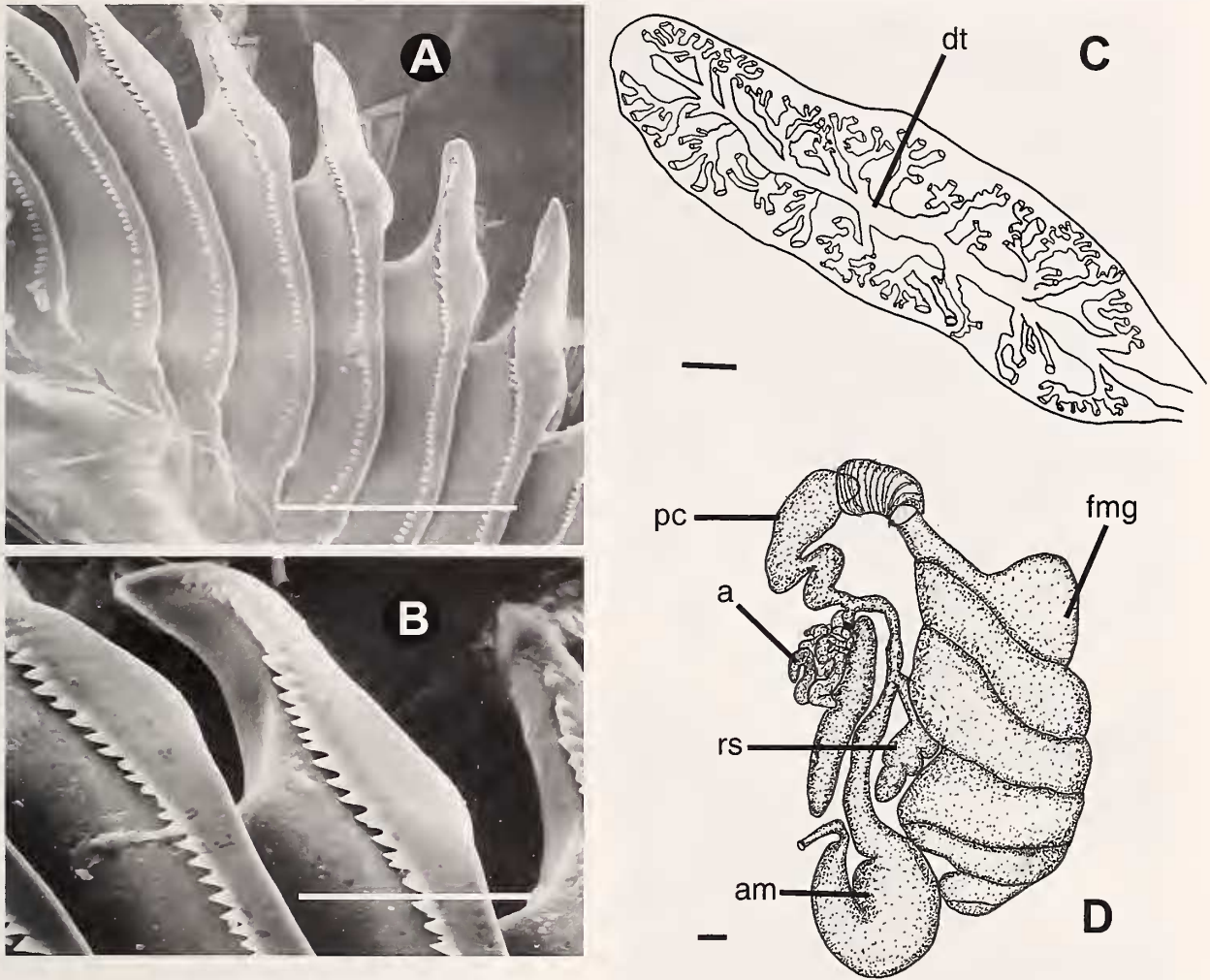


Figure 8. *Phyllodesmium kabiranum*. **A**. Lateral view of radula. **B**. View of radular denticles. **C**. View of digestive tract inside a ceras. **D**. Reproductive system. Abbreviations: a, albumen gland; am, ampulla; rs, receptaculum seminis; pc, penial complex; fmg, female mass gland; dt, digestive tract. Scale bars: **A** = 0.12 mm; **B** = 0.05 mm; **C** = 12 mm; **D** = 5 mm.

to massive, folded, rectangular shaped female gland mass. Female duct opening into a vagina at base of first cereal cluster on right side of dorsum.

Remarks: Baba (1991) considered *Eolida bella* Rüppel & Leuckart, 1831 as a possible senior synonym of *Phyllodesmium*. Baba noted the similarity in color pattern between the two taxa. However, the remainder of the anatomy of *E. bella* remains unknown. Examination of material from the Red Sea is necessary to confirm the identity of *E. bella*, in order resolve this nomenclatural issue.

***Phyllodesmium macphersonae* (Burn, 1962)**

(Figs. 1D, 9A–D)

Cratena macphersonae Burn, 1962: 118–119, figs. 19–20.

Phyllodesmium macphersonae — Rudman, 1981b: 239–242, 244–261, figs. 12A, B, 17, 21C, 27.

Material examined: One specimen, dissected, CASIZ 115724, Horseshoe Cliffs, Okinawa, Ryukyu Islands, Japan, 3.0 m depth, 29 May 1998, R.F. Bolland. One specimen, CASIZ 104700, 14 km W of Ikei-shima, Tengan Pier, Okinawa, Ryukyu Islands, Japan, 2.1 m depth, 26 August 1994, R.F. Bolland.

Distribution: Originally described from Victoria, Australia (Burn, 1962). Recorded from the Coral Sea (Lord Howe Island) and Tasmania, Australia (Rudman, 1991). Also collected from Japan (present study).

External morphology (Fig. 1D): Body 23 mm in length, of moderate size, extending narrowly from the anterior to the posterior end. Anterior end of foot angular,

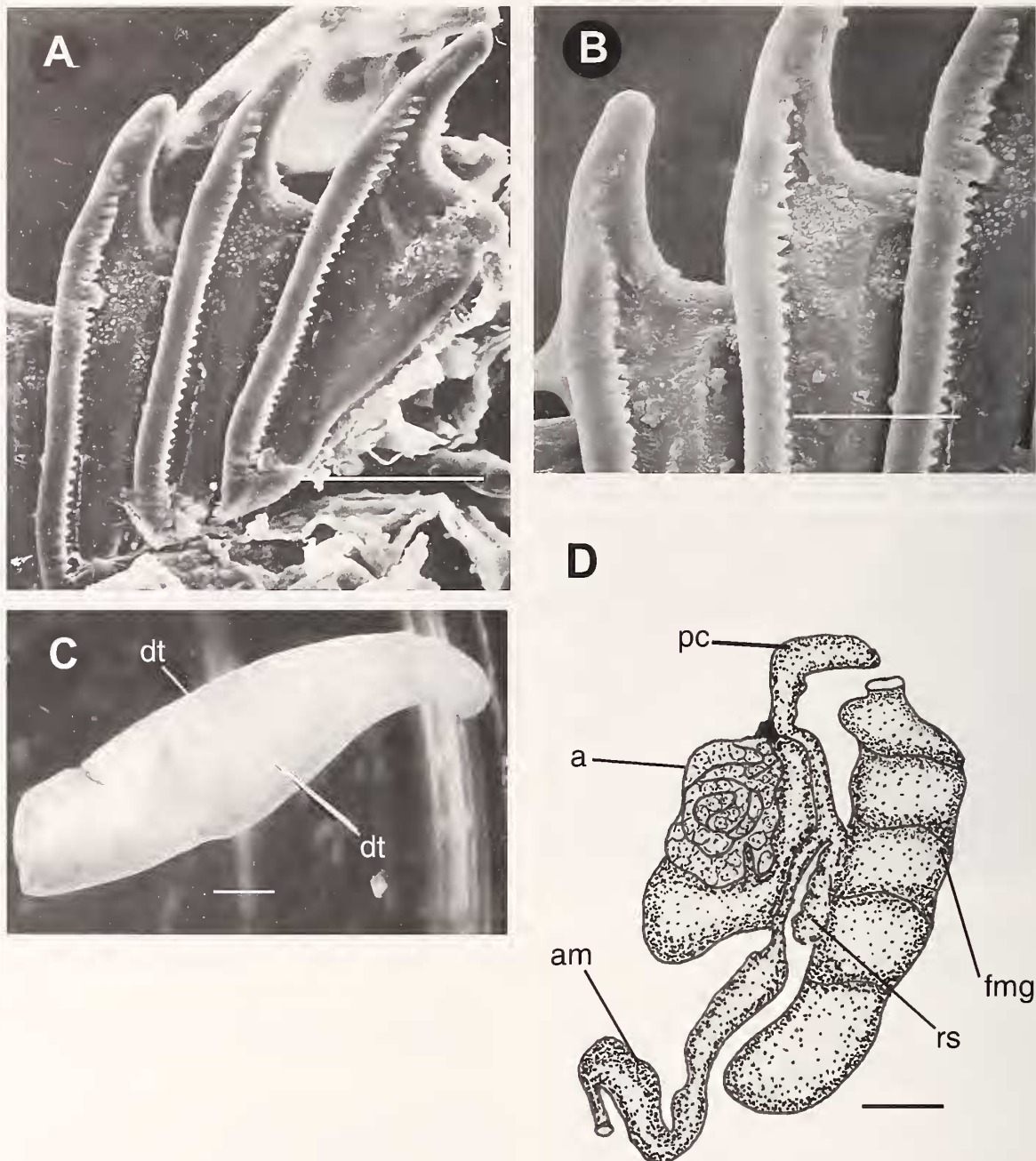


Figure 9. *Phyllodesmium macphersonae*. **A.** Lateral view of radula. **B.** Close up view of radular denticles. **C.** View of digestive tract inside a ceras. **D.** Reproductive system. Abbreviations: a, albumen gland; am, ampulla; rs, receptaculum seminis; pc, penial complex; fmg, female mass gland; dt, digestive tract. Scale bars: **A** = 0.04 mm; **B** = 0.02 mm; **C** = 10 mm; **D** = 5 mm.

narrow, elongate, tapering from the anterior to posterior end. Rhinophores moderately long, smooth, close in size to oral tentacles. Ceratal arrangement of one precardiac arch, up to 6 to 8 single vertical postcardiac rows, up to 6 to 8 cerata on each postcardiac rows on each side of body. Reproductive opening on right side, below anterior basal edge of

precardiac arch. Renal opening immediately above first postcardiac row, in interhepatic space. Anal papilla between first and second postcardiac row, immediately below uppermost postcardiac row.

Cerata and digestive gland (Fig. 9C): Cerata cylindrical, smooth, terminating in curled apex. Digestive

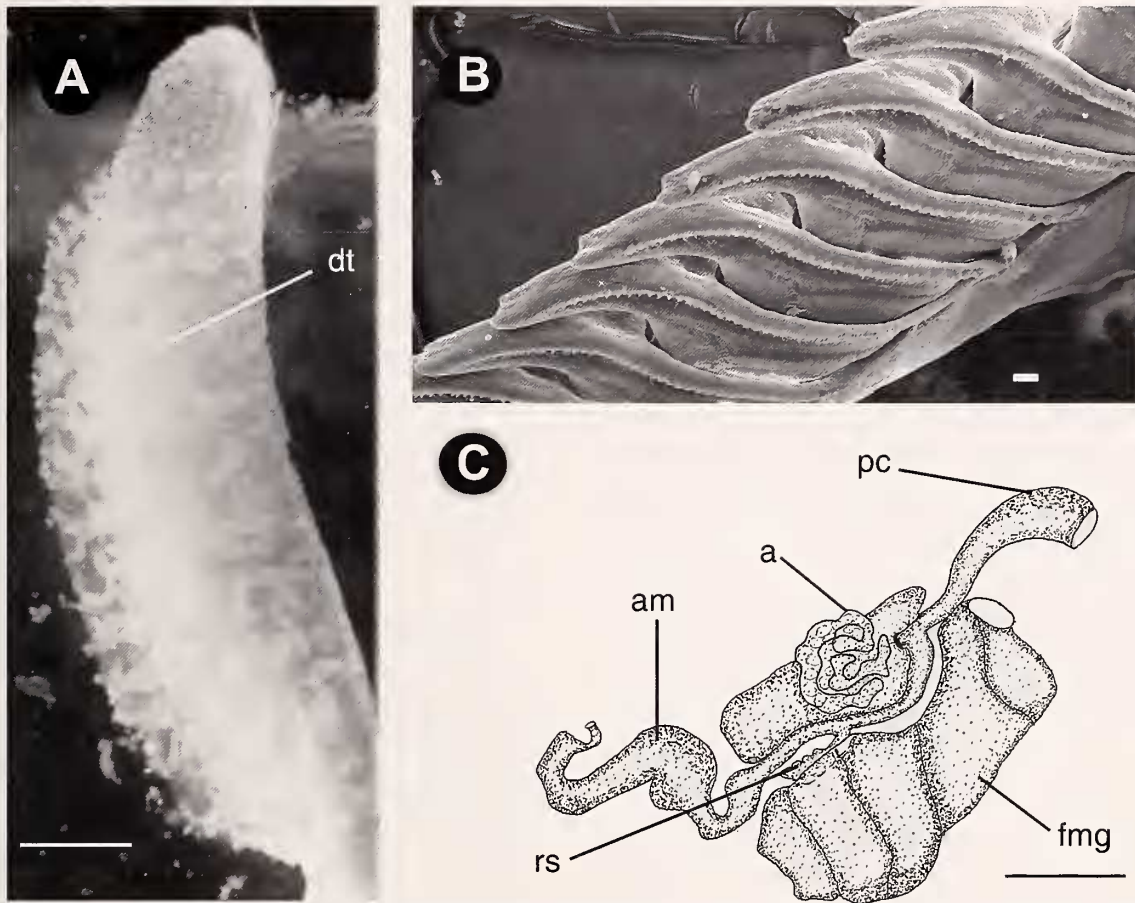


Figure 10. *Phyllodesmium briareum*. **A.** View of digestive tract inside a cerata. **B.** Lateral view of radula. **C.** Reproductive system. Abbreviations: a, albumen gland; am, ampulla; rs, receptaculum seminis; pc, penial complex; fmg, female mass gland; dt, digestive tract. Scale bars: **A** = 10 mm; **B** = 0.01 mm; **C** = 5 mm.

gland composed of central duct running along entire cerata. Photographs of the cerata do not obviously show the detailed structure. However, under close examination through the dissecting microscope, the arrangement of the secondary and tertiary branches was similar to that of *P. magnum*.

Buccal armature (Fig. 9A–B): Radular formula $28 \times 0.1.0$ (CASIZ 65346). Tooth long and narrow base, long cusp. Denticles visible, all along central region of radular teeth, separated, short, terminating in a blunt tip. Masticatory border of jaw smooth (Baba, 1991).

Reproductive system (Fig. 9D): Preampulla narrow, reduced, duct expanding into long and thin ampulla by irregular narrow duct; duct bifurcating into receptaculum seminis and penial complex. Penial complex extending into small and bulbous prostate, which connects to a long, folding and thin female gland mass; female duct opened to a vagina at the base of first ceratal cluster.

Phyllodesmium briareum (Bergh, 1896)

(Figs. 1G, 10A–C)

Ennoia briareus Bergh, 1896: 392–4, Pl. 16, figs. 14, 15.

Phyllodesmium briareus — Gosliner *et al.*, 1996: 177, fig. 627.

Phyllodesmium briareum — Rudman, 1991: 181–187, figs. 13, 14A,B, 15, 16, 17, 27–29.

Material examined: Twenty specimens, CASIZ 065346, Barracuda Point, W side “Pig Island,” near Madang, north coast, Papua New Guinea, 15.2 m depth, 13 January 1988, T.M. Gosliner. One specimen, one dissected, CASIZ 065299, Madang (near lighthouse), north coast, Papua New Guinea, 7.6 m depth, 22 January 1988, T.M. Gosliner. Four specimens, one dissected, CASIZ 83678, Devil’s Point (SW side of Maricaban Island), Maricaban Island, Batangas Province, Luzon, Philippines, 19 February 1992, T.M. Gosliner.

Distribution: Found in the Philippines, Malaysia and Papua New Guinea (Rudman, 1991). Recent studies found *P. briareum* in Japan and Indonesia (present study).

External morphology (Fig. 1G): Body 16 mm in length, moderate size, narrow, reduced (in some cases more elongate). Foot narrow, angular anterior end of corners. Oral tentacles slightly longer than greatly extended rhinophores. Smooth, cylindrical cerata terminating in blunt tip. Ceratal arrangement of one single-rowed precardiac arch, consisting 6 to 8 ceras on each side of body. Reproductive system, renal opening and anal papilla located on right side of body, underneath the precardiac row. Renal opening in the interhepatic space. Anal papilla below first post-cardiac row. Postcardiac cerata in single rows across dorsum on each side of body, each side with 6 to 8 postcardiac clusters with up to 7 ceras on each of them.

Cerata and digestive gland (Fig. 10A): Cerata long, slender, smooth, cylindrical, with branched digestive tract. Digestive tract branching into simple branches, in turn extending into secondary and tertiary branches, making for a dense layer and expansion of the digestive tract all across cerata.

Buccal armature (Fig. 10B): Radular formula $34 \times 0.1.0$ (CASIZ 83678). Base of tooth wide, long, with long cusp. Denticles visible, along central edge of each tooth, short, well-separated, terminating in pointed radular tip. Masticatory border of jaw smooth (Rudman, 1991).

Reproductive system (Fig. 10C): Preampullary duct short, narrow, expanding into bulbous, long and folded ampulla. Ampulla connecting through broad duct to receptaculum seminis and penial complex. Penial complex opening to wide and short prostate through broad duct. Duct connecting to folded albumen gland, located on massive membrane gland. Prostate connecting into folded and long female gland mass.

Phyllodesmium longicirrum (Bergh, 1905)

Myrrhine longicirra Bergh, 1905: 227–9, Pl. 20, figs. 20–29.

Phyllodesmium longicirra — Rudman, 1981b: 242–261, figs. 16, 18–20, 24–27.

Phyllodesmium longicirrum — Rudman, 1991: 195, figs. 26, 28, 29.

Distribution: Described originally from Indonesia (Bergh, 1905), also recorded from the Great Barrier Reef (Rudman, 1991).

Discussion: The anatomy of this species has been described by Rudman (1981b; 1991).

Phyllodesmium pecten Rudman, 1981

Phyllodesmium pecten Rudman, 1981b: 237–239, figs. 14A, 15, 16C, D, E, 27.

Distribution: Known only from its type locality Dar es Salaam, Tanzania (Rudman, 1981b).

Discussion: Anatomy of species described by Rudman, 1981b.

Phyllodesmium opalescens Rudman, 1991

Phyllodesmium opalescens Rudman, 1991: 177–181, figs. 9, 10, 11, 12, 28, 29.

Distribution: Known only from its type locality Hong Kong (Rudman, 1991).

Discussion: Anatomy of species described by Rudman, 1991.

Phyllodesmium horridum (Macnae, 1954)

Favorinus horridus Macnae, 1954: 19–21, figs. 11–13, Pl. 1, fig. 4.

Phyllodesmium horridum — Risso-Dominguez, 1964: 222–238.

Phyllodesmium horridum — Rudman, 1981b: 224.

Phyllodesmium horridum — Gosliner, 1987: 124, fig. 225.

Distribution: Known and described originally from South Africa (Macnae, 1954).

Discussion: Anatomy of species described by Rudman (1981b; 1991).

Phyllodesmium iriomotense Baba, 1991

Phyllodesmium iriomotense Baba, 1991b: 115, figs. 6–7, Pl. 1, fig. 3.

Distribution: Known only from its type locality Okinawa, Japan (Baba, 1991b).

Discussion: Anatomy of species described by Baba, 1991b.

Phyllodesmium guamensis Avila et al., 1998

Phyllodesmium guamensis Avila et al., 1998: 148, figs. 1–10.

Distribution: Only found in its type locality Guam (Micronesia) (Avila et al., 1998).

Discussion: Anatomy of species described by Avila et al., 1998

***Phyllodesmium jakobsenae* Burghardt & Wägele,
2004**

Phyllodesmium jakobsenae Burghardt & Wägele, 2004:
1, figs. 1–5.

Distribution: Known only from Indonesia (Burghardt & Wägele, 2004).

Discussion: The anatomy of this species was completely described by Burghardt & Wägele (2004).

***Phyllodesmium rudmani* Burghardt & Gosliner,
2006**

Phyllodesmium jakobsenae Burghardt & Gosliner, 2006:
31, figs. 1–5.

Distribution: Known only from Indonesia (Burghardt & Gosliner, 2006).

Discussion: The anatomy of this species was completely described by Burghardt & Gosliner (2006).

***Godiva quadricolor* (Barnard, 1927)**

Hervia quadricolor Barnard, 1927: 203, Pl. 20, figs. 9,
10.

Godiva quadricolor — Macnae, 1954: 23–25, text figs.
14–16.

Distribution: This species has been collected from South Africa (Barnard, 1927) and Western Australia (Willan, 1987).

Discussion: Anatomy of species described by Willan (1987). *Godiva* Macnae has been placed on the Official List of Generic Names in Zoology with the name number 1717 (I.C.Z.N., 1966, Opinion 778). The name *quadricolor* Barnard, as published in the binomen *Hervia quadricolor* (type species of *Godiva* Macnae), has been placed in the Official List of Specific Names in Zoology with name number 2148 (I.C.Z.N., 1966, Opinion 778).

***Favorinus japonicus* Baba, 1949**

Favorinus japonicus Baba, 1949: 177, Pl. 43, fig. 151,
figs. 135–136.

Distribution: Have been found in Dar es Salaam, Tanzania (Rudman, 1980) and Japan (Baba, 1949) and throughout the Indo-Pacific, extending from the Western Indian Ocean to the Hawaiian Islands (Gosliner, 1980).

Discussion: Anatomy of species described by Baba (1949) and Rudman (1980).

RESULTS

We performed several analyses of the data matrix (Table 3). After several iterations we re-examined the characters. Three characters (14, 21 and 30) were then deleted (using PAUP 4.0 and manually) from the analysis because they are continuous and it is difficult to assess discrete character states. This analysis yielded two trees of 64 steps and consistency and retention indices of 0.469 and 0.730 respectively (Fig. 11). From this analysis, the monophyly of *Phyllodesmium* is supported. Our strict consensus tree shows *Phyllodesmium* as a monophyletic group, supported by a Bremer value of 2 and defined by four synapomorphies: character 12, angular foot corners; character 15, rhinophores smooth or slightly nodular; character 16, masticatory border with a single row of denticles; character 27, cnidosac absent (Fig. 12). Most nodes have a Bremer support value of 1. The third node above the basal node has a value of 3. Additionally, the clade that contains *P. poindinniei*, *P. briareum*, *P. macphersonae* and *P. colemani*, the clade that contains *P. magnum*, *P. longicirrum*, *P. guamensis*, *P. paramagatum*, *P. jakobsenae* and *P. rudmani* and the clade containing *P. hyalinum* and *P. crypticum* each have a value of 2.

Our phylogenetic analysis shows that species possessing an unbranched digestive tract (*P. horridum*, and *P. opalescens*) are most basal, while others that have a branched digestive tract are more derived. *Phyllodesmium* species having a branched digestive tract are included in one clade, indicating that elaboration of the digestive gland duct represents a single evolutionary event. Members of this clade share other common traits relating to jaw morphology, ceratal structure, and their ability to store zooxanthellae. Within this group, there is one well-supported clade that divides into two sister clades. The first one is supported by one synapomorphy (narrow foot), while the second is supported by two synapomorphies (ceratal apex curled and tightly congested radular denticles).

Based on the present phylogenetic analysis, some characters used in this study exhibit at least one instance of reversal (indicated by an underline of the character number in Figure 12). Even though the instances of homoplasy are moderate, the phylogenetic reconstruction of the ancestral state is unambiguous. Figure 12 shows some of the characters displaying homoplasy, such as the presence of character 2 in several taxa within different lineages. Several derived characters support distinct phylogenetic relationships within various subclades of *Phyllodesmium*. These derived characters include the presence of zooxanthellae, ceratal morphology (apex, surface, shape) and ceratal arrangement, digestive tract branching, and masticatory border of jaw. Tracing of character trace

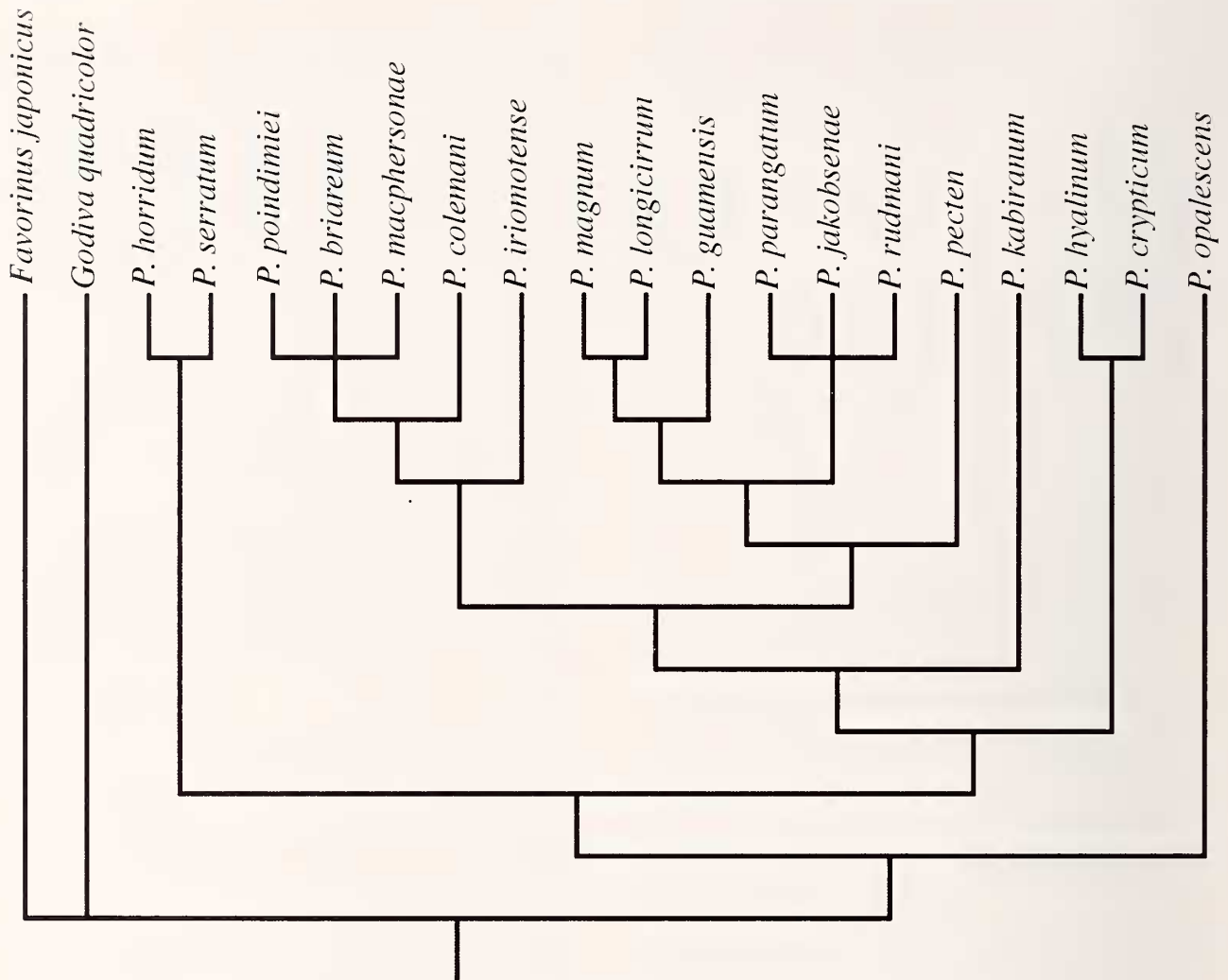


Figure 11. Strict consensus phylogeny of *Phyllodesmium*, (characters 14, 21, 30 excluded).

evolution was made on the not fully resolved consensus tree rather than on one of the two fully resolved trees produced by the phylogenetic analysis. This approach emphasizes the distribution of characters that are consistent rather than those that vary.

DISCUSSION

The phylogenetic analysis carried out in this paper supports the monophyly of the exclusively tropical Indo-Pacific species that have been included in *Phyllodesmium*. In general, the non-parsimony based scenario of evolution suggested by Rudman (1991) is generally upheld by the present phylogenetic analysis. More specifically, our parsimony-based phylogeny supports Rudman's view that more basal members have relatively simple digestive gland branching and more derived taxa have more complex branching of

digestive gland ducts to provide greater surface area for photosynthesis in species that harbor zooxanthellae. However, the arrangement of taxa within Rudman's branching diagram differs in some respects from our phylogeny. For example, Rudman suggested that *P. serratum* was most basal within *Phyllodesmium*, while our analysis suggests that *P. opalescens* is more basal. Additionally, Rudman suggested a continuum of evolution from *P. crypticum* to *P. hyalinum* to *P. pecten*, whereas our analysis suggests that *P. crypticum* and *P. hyalinum* are sister species, while *P. pecten* is a member of another subclade.

Rudman treated evolution within *Phyllodesmium* based on the comparative examination of the digestive system and cerata. However, it is hard to assess how related these assumptions are due to insufficient data regarding the specificity of the feeding specialization across all *Phyllodesmium* taxa. It is evident, though,

photographs used in this study. Also thanks to Dr. Gary Williams, Dr. Ángel Valdés, Erin Rempala, Elizabeth Ruck and Yvonne Valles in the Invertebrate Zoology and Geology Department of the California Academy of Sciences, and Dr. Thomas Niesen at San Francisco State University for their guidance, support and comments through the preparation of this manuscript. Above all, the senior author would like to thank her family and friends for their patience, love and encouragement.

LITERATURE CITED

- AVILA, C., M. BALLESTEROS, M. SLATTERY & V. J. PAUL. 1998. *Phyllodesmium guamensis* (Nudibranchia, Aeolidioidea), a new species from Guam (Micronesia). *Journal of Molluscan Studies* 64:147–160.
- BABA, K. 1937. Opisthobranchia of Japan (II). *Journal of the Department of Agriculture Kyushu Imperial University* 5: 289–344.
- BABA, K. 1949. Opisthobranchia of Sagami Bay collected by his Majesty the Emperor Japan. first edition, 194 pp, 50 pls. Iwanami Shoten: Tokyo.
- BABA, K. 1955. Opisthobranchia of Sagami Bay, Supplement, 59 pp, 20 pls. Iwanami Shoten: Tokyo.
- BABA, K. 1990. Nomenclatural review of the species treated in "Opisthobranchia of Sagami Bay" (1949). In: Opisthobranchia of Sagami Bay collected by his Majesty the Emperor Japan. Second edition, 211 + 13 pp, 50 pls. Iwanami Shoten: Tokyo.
- BABA, K. 1991a. The Anatomy of *Phyllodesmium serratum* (Baba, 1949) from Japan (Nudibranchia: facelinidae). *Venus* 50(2):101–108.
- BABA, K. 1991b. Taxonomical study on some species of the genus *Phyllodesmium* from Cape Muroto-misaki, Shikoku and Okinawa Province, Southern Japan (Nudibranchia: facelinidae). *Venus* 50(2):109–123.
- BARNARD, K. H. 1927. South African nudibranch Mollusca, with descriptions of new species, and a note on some specimens from Tristan d'Acunha. *Annual of the South African Museum* 25:171–215.
- BERGH, L. S. R. 1896. Eolidiens d'Amboine. *Voyage de MM. M. Bedot et C. Pictet dans l'Archipel Malais. Revue Suisse de Zoologie* 4:385–394, Pl. 16.
- BERGH, L. S. R. 1905. Die Opisthobranchiata. *Siboga Expeditie Report* 50:1–248.
- BREMER, K. 1994. Branch support and tree stability. *Cladistics* 10:295–304.
- BURGHARDT, I., J. EVERTSEN, G. JOHNSEN & H. WÄGELE. 2005. Solar powered seaslugs – Mutualistic symbiosis of aeolid Nudibranchia (Mollusca, Gastropoda, Opisthobranchia) with *Symbiodinium*. *Symbiosis* 38:227–250.
- BURGHARDT, I. & T. GOSLINER. 2006. *Phyllodesmium rudmani* (Mollusca: nudibranchia: aeolidioidea), a new solar powered species from the Indo-West Pacific with data on its symbiosis with zooxanthellae. *Zootaxa* 1308: 31–47.
- BURGHARDT, I. & H. WÄGELE. 2004. A new solar powered species of the genus *Phyllodesmium* Ehrenberg, 1831 (Mollusca, Nudibranchia: aeolidioidea) from Indonesia with analysis of its photosynthetic activity and notes on biology. *Zootaxa* 596:1–18.
- BURGHARDT, I. & H. WÄGELE. 2006. Interspecific differences in the efficiency and photosynthetic characteristics of the symbiosis of "solarpowered" Nudibranchia (Mollusca: gastropoda) with zooxanthellae. *Records of the Western Australian Museum* 69:1–9.
- BURN, R. 1962. Descriptions of Victorian nudibranchiate Mollusca, with a comprehensive review of the Eolidacea. *Memoirs of the Natural Museum of Melbourne* 25:95–128.
- COLEMAN, N. 1988. Fauna Survey Lord Howe Island, October 87. *Underwater* 23:14–15.
- EHRENBERG, G. G. 1831. *Symbolae Physicae seu icones est descriptiones animalium evertebratorum sepositis insectis quae ex itinere per Agricam Borealem et Asiam Occidentalem. Decas I Mollusca.*
- ELIOT, C. N. E. 1905. On some nudibranchs from East Africa and Zanzibar. Part 6. *Proceedings of the Zoological Society of London* 2:268–298.
- ENGEL, H. & C. J. VAN EKEN. 1962. Contributions to the knowledge of the Red Sea, No. 22. Red Sea Opisthobranchia from the coast of Israel and Sinai. *Bulletin of the Israel Ministry of Agriculture, Division of Fisheries, Sea Fisheries Research Station* 30:15–34.
- FANKBONER, P. V. 1971. Intracellular digestion of symbiotic zooxanthellae by host amoebocytes in giant clams (Bivalvia, Tridacnidae) with a note on the nutritional role of the hypertrophied siphonal epidermis. *Biological Bulletin* 141:222–234.
- FITT, W. K. & R. K. TRENCH. 1981. Spawning, development and acquisition of zooxanthellae by *Tridacna squamosa* (Mollusca, Bivalvia). *Biological Bulletin* 161:213–235.
- GOHAR, H. A. F. & I. A. ABUL-ELA. 1957. On a new nudibranch "*Phyllodesmium xeniae*" (from the Red Sea, with a description of its development). *Publications of the Marine Biological Station Al Ghardaga, Egypt* 9:131–144, pls. 1–2.
- GOREAU, T. F., N. I. GOREAU & C. M. YONGE. 1973. On the utilization of photosynthetic products from zooxanthellae and of a dissolved amino acid in *Tridacna maxima f. elongata* (Mollusca, Bivalvia). *Journal of Zoology (London)* 169:417–454.
- GOSLINER, T. M. 1980. The systematics of the Aeolidacea (Nudibranchia: gastropoda) of the Hawaiian Islands with the description of two new species. *Pacific Science* 33:37–77.
- GOSLINER, T. M. & M. T. GHISELIN. 1984. Parallel evolution in opisthobranch gastropods and its implication for phylogenetic methodology. *Systematic Zoology* 33:255–274.
- GOSLINER, T. M. 1987. Nudibranchs of Southern Africa, a guide to the Opisthobranchs of southern Africa, 136 pp, Sea Challengers: Monterey.
- GOSLINER, T. M., D. W. BEHRENS & G. C. WILLIAMS. 1996. *Coral Reef Animals of the Indo-Pacific*, 314 pp, Sea Challengers: Monterey.
- GRAY, J. E. 1847. The classification of the British Mollusca. *Annals & Magazine of Natural History* 20:267–273.
- HOEGH-GULDBERG, I. O. & R. HINDE. 1986. Studies on a nudibranch that contains zooxanthellae 1. Photosynthesis, respiration and the translocation of newly fixed carbon by zooxanthellae in *Pteraeolidia ianthina*. *Proceedings of the Royal Society, London, B* 228:493–509.
- KEMPF, S. C. 1984. Symbiosis between the zooxanthellae *Symbiodinium* (= *Gymnodinium*) *microadriaticum* (Freudenthal) and four species of nudibranchs. *Biological Bulletin* 166:110–126.
- MACNAE, W. 1954. On some aeolidacean nudibranchiate

- molluscs from South Africa. *Annals of the Natural Museum* 13:1–50.
- MADDISON, W. P. & D. R. MADDISON. 1992. MacClade: analysis of Phylogeny and Character Evolution. Version 3.0. Sinauer Associates: Sunderland, Massachusetts.
- MILLER, M. C. 1971. Aeolid nudibranchs (Gastropoda: opisthobranchia) of the family Glaucidae from New Zealand Waters. *Zoological Journal of the Linnean Society* 60:197–222.
- MILLER, M. C. 1974. Aeolid nudibranchs (Gastropoda: opisthobranchia) of the family Glaucidae from New Zealand Waters. *Zoological Journal of the Linnean Society* 54:31–61.
- ODHNER, N. H. 1934. The Nudibranchia. British Antarctic "Terra Nova" Expedition, 1910-13, Reports, *Zoology* 7: 229–310.
- O'DONOGHUE, C. H. 1929. Report on the Opisthobranchiata. Results of the Cambridge Expedition to the Suez Canal, 1924. *Transactions of the Zoological Society of London* 22:713–841.
- ORR, J. 1981. Hong Kong nudibranchs, 82 pp, Urban Council: Hong Kong.
- ORTIZ, D. M. 2001. Phylogeny and ecological interactions of facelinid nudibranch genus *Phyllodesmium* and Indo-Pacific coelenterates. M.A. Thesis, San Francisco State University: San Francisco. 88 pp.
- ORTIZ, D. M. & T. M. GOSLINER. 2003. A new species of *Phyllodesmium* Ehrenberg, 1831 (Mollusca, Nudibranchia) from the Tropical Indo-Pacific. *Proceedings of the California Academy of Sciences* 54:161–168.
- RISBEC, J. 1928. Contribution à l'étude des nudibranches Néocalédoniens. *Faune des Colonies Françaises* 2:1–328, pls A–D, 1–12.
- RISBEC, J. 1953. *Mollusques nudibranches de la Nouvelle-Calédonie*. Office de la recherche scientifique outre-mer, Paris, 1–189.
- RISSO-DOMINGUEZ, C. J. 1964. Notes on the Facelinacea. 2. On the systematic position of *Hervia serrata* Baba, 1949 and *Favorinus horridus* Macnae, 1954 (Mollusca Nudibranchia). *Beaufortia* 10:222–238.
- RUDMAN, W. B. 1980. Aeolid opisthobranch molluscs (Glaucidae) from the Indian Ocean and the south-west Pacific. *Zoological Journal of the Linnean Society* 68:139–172.
- RUDMAN, W. B. 1981a. Further studies on the anatomy and ecology of opisthobranch mollusks feeding on the scleractinian coral *Porites*. *Zoological Journal of the Linnean Society* 71:343–412.
- RUDMAN, W. B. 1981b. The anatomy and biology of alcyonarian-feeding on aeolid opisthobranch molluscs and their development of a symbiosis with zooxanthellae. *Zoological Journal of the Linnean Society* 72:219–262.
- RUDMAN, W. B. 1982. The taxonomy and biology of further aeolidacean and arminacean nudibranch molluscs with symbiotic zooxanthellae. *Zoological Journal of the Linnean Society* 74:147–196.
- RUDMAN, W. B. 1987. Solar powered animals. *Journal of Natural History* 96:50–53.
- RUDMAN, W. B. 1991. Further studies on the taxonomy and biology of the octocoral-feeding genus *Phyllodesmium* Ehrenberg, 1831 (Nudibranchia: aeolidacea). *Journal of Molluscan Studies* 57(2):167–203.
- RÜPPELL, W. P. & E. S. LEUCKART. 1831 (for 1828). Neue wirbellose Thiere des Rothen Meers. In: *Atlas zu der Reise im nördlichen Afrika von Eduard Rüppell*, 5, Pp. 1–47 pls 1–12. Heinr. Ludw. Brönnner, Frankfurt am Main.
- SWOFFORD, D. L. 2001. PAUP*. *Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates: Sunderland, Massachusetts.
- WILLAN, R. C. & N. COLEMAN. 1984. Nudibranchs of Australasia, 56 pp. *Australasian Marine Photographic Index*: Sydney.
- WILLAN, R. C. 1987. Phylogenetic systematics and zoogeography of Australian nudibranchs. 1. Presence of the aeolid *Godiva quadricolor* (Barnard) in Western Australia. *Journal of the Malacological Society of Australia* 8:71–85.